University of Alberta

DECLINES IN THE BLACK-THROATED GREEN WARBLER (*DENDROICA VIRENS*): FROM PATTERN TO PROCESS

by

Theresa A. Hannah

©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Conservation Biology

Department of Renewable Resources

Edmonton, Alberta

Spring 2006

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-494-13820-3
Our file Notre référence
ISBN: 0-494-13820-3

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

ABSTRACT

The black-throated green warbler (*Dendroica virens*) is listed as a species of concern in Alberta due to projected loss of habitat and reduction in habitat quality. Local populations declined by 50% in experimentally isolated forest fragments 5 years following harvest at Calling Lake, AB, but subsequent declines in controls contributed to convergence at reduced levels 11 years after harvest. Patch occupancy by black-throated green warblers over an 11-year period (1994-2004) was related to forest structure and pre-harvest abundance, with only a weak relationship to patch size and fragmentation. Territory size and fitness measures were similar between fragments and controls 10-11 years post-harvest, although total potential reproductive output was higher in controls. Edge avoidance and area effects were apparent in forest fragments. Selection for older mixedwood forests was confirmed at multiple spatial scales. Older mixedwood stands are at risk due to current forestry practices in Alberta, and regional habitat loss may have contributed to the overall local population decline of 70% for the black-throated green warbler at Calling Lake.

ACKNOWLEDGEMENTS

Throughout this process, the support and encouragement I consistently received was my lifeline. To all, I am eternally grateful. I must begin by thanking my supervisor, Fiona Schmiegelow, for gently persuading me to do this degree in the first place, for nurturing me professionally, and for granting me the freedom to explore my own ideas. My committee members, Susan Hannon and Steve Cumming, were wonderful sounding boards, and assisted me in moulding this project from day one. Lee Foote's comments as external examiner also improved the final version of this thesis.

I feel privileged to have experienced the wonder and beauty of the boreal forest at Calling Lake. My heartfelt thanks to Fiona for introducing me to the boreal and giving me the opportunity to spend so much time there, and to Kevin for sharing his knowledge and passion, and opening my eyes to the magic contained in every minute detail.

I am grateful to the myriads of dedicated field workers who collected the point count data, all of whom endured bugs, mud, thorns and bears, to reveal the intricacies of the avian community. My project involved some wonderful field assistants whose passion and interest in the secret life of the black-throated green warbler was both inspirational and motivational: R.A. Ball, C. Boulton, W. Fleming, J. Gorton, M. Hindle, D. Keeping, J. Martin-Demoor, C. Morcos, B. Olsen, R. Pennell, S. Smith, K. St.-Laurent, and J. Thompson. Thanks for blindly running through the alder and gooseberry in pursuit of the far-off song, in the hopes of catching a glimpse of our elusive subjects. I hope your knees are finally thorn-free, and your necks pain-free after staring at the canopy for weeks on end. I also want to thank K. Morrison, J. Martin-Demoor and G. Berg for sharing my excitement during the pilot year when we found Fen and Bog's nest – that summer fuelled the flames of this project, and I'm glad you were all there with me.

My lab mates were always there for brainstorming sessions, critical discussions, and to blow off some steam. Thanks for your generosity of spirit, and for lightening my burden by sharing the load. K. Lisgo, L. Young, T. Gartner, S. Rudyk and S. Slater made these years more efficient and stress-free, by providing assistance whenever necessary without hesitation. I am also grateful to those outside my lab who offered their time and wisdom to get me over hurdles related to field work, GIS, and statistics: P. Blenis, N. Koper, M. Krawchuk, B. Hantel, C. McCallum and C. Nielson.

Thanks to K. Hannah and K. Lisgo who volunteered to run around the woods with me in the fall to find and GPS lost flagged trees. K. Hannah, L. Young, and of course Fiona were editors supreme – thanks so much for taking the time; your constructive criticism and insightful comments greatly improved the quality of this thesis.

This research was supported by NSERC IPS, ACA Grants in Biodiversity, Alberta Sport, Recreation, Parks and Wildlife Foundation, Edmonton Bird Club, J Gordin Kaplan Graduate Student Award, Graduate Students' Assoc. Professional Development Grant, Government of Alberta Graduate Student Scholarship, and the Department of Renewable Resources, U of A. Alberta-Pacific Forest Industries, particularly Elston Dzus, was my industrial sponsor, and provided support throughout my degree.

My family's love and support was unwavering, and ever appreciated. Cindy McC, for always believing in me, I thank-you. And to Kevin, I am forever indebted to you. You are my inspiration, and my rock.

TABLE OF CONTENTS

DECLINES IN THE BLACK-THROATED GREEN WARBLER: INTRODUCTION 1

1.1 Scope and Rationale 1
1.2 Natural History 3
1.3 Thesis Overview 4
1.4 Literature Cited 5

DECLINES IN THE BLACK-THROATED GREEN WARBLER: PATTERN 9

2.1 Introduction 9
2.2 Methods 12
2.2.1 Study Area 12
2.2.2 Experimental Design 12
2.2.3 Point Counts 13
2.2.4 Statistical Analyses 16
2.2.4.1 Population trend 16
2.2.4.2 Patch occupancy 16
2.3 Results 19
2.3.1 Population Trend 19
2.3.2 Patch Occupancy 21
2.4 Discussion 22
2.4.1 Population trend 22
2.4.2 Patch Occupancy 25
2.4.3 Broader Determinants of the Local Decline 28
2.4.4 Conservation and Management Implications 29
2.5 Literature Cited 31

DECLINES IN THE BLACK-THROATED GREEN WARBLER: PROCESS 38

3.1 Introduction 38
3.2 Methods 41
3.2.1 Study Area 41
3.2.2 Point counts 42
3.2.3 Population-level Surveys 42
3.2.4 Vegetation Sampling 45
3.2.5 Territory Delineation 46
3.2.6 Spatial Analyses 47
3.2.7 Statistical Analyses 49
3.2.7.1 Area effects 49
3.2.7.2 Edge Effects 50
Vegetation Selection and Vegetation Change 50
Edge Avoidance 50
3.2.7.3 Habitat Quality 51

3.3 Results **51**
3.3.1 Area Effects 51
3.3.2 Edge Effects 54
3.3.2.1 Vegetation Selection and Vegetation Change 54
i. Vegetation Selection: Territory-level 54
ii. Vegetation Selection: Stand-level 55
iii. Vegetation Change: Selected Attributes 56
3.3.2.2 Edge Avoidance 57
3.3.3 Habitat Quality 58
3.4 Discussion **58**
3.4.1 Area effects 69
3.4.2 Edge Effects 69
3.4.2.1 Vegetation Selection and Change 69
Comparison with Other Regions 72
3.4.2.2 Edge Avoidance 73
3.4.3 Habitat Quality 75
3.4.4 Conservation and Management Implications 77
3.5 Literature Cited **79**

DECLINES IN THE BLACK-THROATED GREEN WARBLER: CONCLUSION **88**

4.1 Thesis Summary **88**
4.2 Management recommendations **90**
4.3 Future research **92**
4.3.1 Calling Lake Black-throated Green Warbler Research 92
4.3.2 Additional Black-throated Green Warbler Research 93
4.4 Literature Cited **95**

LIST OF FIGURES

Figure 2.1 Location of the Calling Lake Fragmentation Experiment study area, in Canada and Alberta, denoted by the star. **14**

Figure 2.2 Spatial layout of the point count stations (n=180) within the Calling Lake Fragmentation Experiment study area; fragment sites are isolated by cutblocks (white) and control sites are embedded within a continuous forest matrix (grey). **14**

Figure 2.3 Population trend of black-throated green warblers in Fragment sites and Control sites from 1993-2004. Data represent annual average abundance from point counts summed by treatment. Asterisks denote significance at α= 0.10 from a repeated measures analysis of variance with contrasts; error bars denote 90% confidence intervals. **20**

Figure 2.4 Partial residual plots of parameters included in the top generalized linear model describing occupancy of black-throated green warblers at point count stations from 1994-2004 in the Calling Lake Fragmentation Experiment; a = average abundance of birds per station in 1993, pre-harvest; b = 2nd order polynomial of area-weighted stand age; c = log transformed area-weighted percent of white spruce in the overstory. **24**

Figure 3.1 Schematic of vegetation sampling within a black-throated green warbler territory. Small, open circles are available trees, light grey are flagged trees (used), of which ~5 per territory were randomly selected (black circles). All available trees ≥8-cm within an 11.3-m radius circle (hatched) surrounding the used trees had species and dbh recorded. **46**

Figure 3.2 Linear regressions depicting average abundance per point count station of black-throated green warblers for each size x treatment category. First data point (1993) is pre-harvest, followed by 11 years of post-harvest data. C=controls, F=fragments. **53**

Figure 3.3 Frequency histograms of the number of vegetation plots with occurrence of paper birch stems; a) within black-throated green warbler territory plots sampled in 2003/2004; b) within point count plots located throughout the study area sampled in 1993 c) within point count plots located throughout the study area sampled in 2003 ..... **66**

Figure 3.4 Four black-throated green territories in a 40-ha Control site. Territory boundaries for 2003 (triangles) and 2004 (circles) are delineated by 95% minimum convex polygons. The thicker black line bisecting image is the eastern site boundary; thinner black lines are Alberta Vegetation Inventory stand boundaries. **67**

LIST OF TABLES

Table 2.1 Independent variables used in a generalized linear model describing occupancy of point count stations by black-throated green warblers from 1994-2004; dependent variable is 'number of years occupied'. **18**

Table 2.2 Results from Repeated Measures ANOVA, with contrasts relative to pre-harvest abundance levels. Bold font denotes a significant difference at α = 0.10 between abundance of black-throated green warblers in fragments and controls in each year compared to the difference that existed in 1993 (pre-harvest). The sign of difference denotes whether fragment levels are higher (+), lower (-), or not significantly different (nd) in relation to control levels.. ..... **21**

Table 2.3 Candidate models describing 'number of years occupied' by black-throated green warblers at the point count station level. *K* specifies the number of parameters in the model, ΔAIC_c indicates the change in value between each model and the model with the lowest AIC_c, and w_i is a weight assigned to the model as a relative likelihood that the model is the best amongst those tested. **23**

Table 2.4 Coefficients, standard errors, and 90% confidence intervals for the terms in the top ranked model describing black-throated green warbler occupancy at Calling Lake point count stations from 1994-2004. ..... **23**

Table 3.1 Reproductive ranks with associated observed behaviours. **44**

Table 3.2 Comparisons of black-throated green warbler abundance estimates in 2003 and 2004 using three methods. **52**

Table 3.3 Results from linear regressions for size x treatment categories. Independent variable is year (1993-2004); dependent variable is average abundance at a point count station. C=Controls, F=Fragments. **53**

Table 3.4 Comparisons of coefficients from linear regressions for size x treatment categories. Independent variable is year (1993-2004); dependent variable is average abundance of black-throated green warblers at a point count station. Results displayed are the p-value followed by the t-statistic in parentheses. C= Controls, F=Fragments; bold denotes significance at a Bonferroni-adjusted alpha of 0.007. ..... **54**

Table 3.5 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use for tree species within black-throated green warbler territories based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected use (+; bold), significantly less than expected use (-; bold) or no difference (0), at $\alpha = 0.10$. **59**

Table 3.6 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use for behaviours associated with tree species within black-throated green warbler territories based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected use (+; bold), significantly less than expected use (-; bold) or no difference (0), at $\alpha = 0.10$. **60**

Table 3.7 Average diameter at breast height (dbh) for used trees (all behaviours combined, n=256) vs. available (n=4534) trees of 4 tree species within black-throated green warbler territories. **60**

Table 3.8 Results of Mann-Whitney U analyses comparing average dbh between used and available trees within black-throated green warbler territories. Comparisons are made within tree species and behaviour. Tests are two-tailed; bold denotes significance at $\alpha = 0.10$. **61**

Table 3.9 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use by black-throated green warblers of dbh size classes of different tree species. Comparisons are between territories and available stands, based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected (+; bold), significantly less than expected (-; bold) or no difference (0), at $\alpha = 0.10$. .. **62**

Table 3.10 Summary statistics and results from case-controlled logistic regression comparing occupied black-throated green warbler territories to random territories within all sites in the study area (Random Landscape), and to territories randomly placed within the originating site (Random Site). **63**

Table 3.11 Results from Wilcoxon-Signed ranks test evaluating vegetation change from 1993/94 to 2003 for vegetation attributes selected by black-throated green warblers. Direction over time refers to a significant increase (↑) or decrease (↓), or no change (0) in abundance levels of the vegetation attribute. **64**

Table 3.12 Estimated mean density and basal area of paper birch (15.0-38.0 cm dbh) at point count vegetation plots located throughout the study area, sampled in 1993/94 and 2003, and within black-throated green warbler territory plots sampled in 2004. Chi-square values evaluate distribution of stems across vegetation plots compared to a normal distribution. **65**

Table 3.13 Summary of edge avoidance results comparing average distance of black-throated green warbler territory boundaries to nearest site edge between fragments and controls (MCP), and of average distance of point locations to nearest site edge between used and random points, for fragments and controls (Points)..... 67

Table 3.14 Summary of tracking episodes for 2003 & 2004 combined, for each treatment. Territory is defined as a territorial male with a minimum of 25 locations across 3 visits each a minimum 10 days apart; n=39..... 68

Chapter 1

DECLINES IN THE BLACK-THROATED GREEN WARBLER: INTRODUCTION

1.1 SCOPE AND RATIONALE

Populations of many songbirds in North America have been declining for several decades, with habitat loss and habitat fragmentation as primary contributing factors (Robbins et al. 1989, Böhning-Gaese et al. 1993, Robinson et al. 1995). Industrial forestry in the western boreal forest, a leading cause of habitat fragmentation (Schmiegelow et al. 1997), is increasing, with little knowledge of long-term ecosystem effects. In Alberta, allocation of >50% of forested land in the province to forestry companies has raised concerns over forest bird populations, among other non-timber values. One predictable consequence of current forestry practices is an increase in fragmentation of remnant patches of older forest, which may have negative consequences for interior forest specialists (Schmiegelow and Hannon 1993). Island biogeography theory predicts that smaller, isolated areas support both fewer species and fewer individuals (MacArthur and Wilson 1967). This phenomenon, when associated with forested systems experiencing fragmentation, has been attributed to area effects, whereby smaller patch sizes reduce songbird abundance or productivity (Zanette 2000), edge effects, which can alter patch microclimate and vegetation structure (Harper et al. 2005), and isolation, which can affect songbird dispersal and recolonization (Gobeil and Villard 2002). These factors may influence habitat quality, and since songbirds seek optimal habitat for breeding, their distribution pattern can assist in identifying higher quality sites (Hames et al. 2001, Thompson 2004). However, relationships between occupancy and

landscape metrics, while effective for predicting bird habitat suitability (Brotons et al. 2004), should be combined with detailed habitat and population surveys to identify songbird response to habitat change (Donovan et al. 1995).

Carignan and Villard (2002) maintain that birds can be effective indicators of ecosystem change, as they respond across many spatial scales, are easy to detect and identify based on vocalizations, and can be efficiently surveyed over large areas. Different adaptations, such as migratory strategies, habitat associations, and diet specializations, ensure that various assemblages which cover a wide range of needs are represented, each of which may differ in their response to habitat alterations (Hobson and Bayne 2000). In 1992, a large-scale fragmentation experiment was established in the mixedwood boreal forest of northern Alberta to determine the effects of forest fragmentation on the songbird community, by monitoring species richness and turnover, as well as species-specific abundance levels over time (Schmiegelow and Hannon 1993, Schmiegelow et al. 1997). Surveys have been conducted from one year pre-harvest (1993) to 11 years following harvest (2004), to record changes in the songbird population in isolated forest fragments compared to continuous control forests. One forest interior songbird, the black-throated green warbler (*Dendroica virens*), experienced a crowding effect (Hagan et al. 1996) in isolated forest fragments one-year post-harvest, followed by a significant decline for the following 4 years, resulting in abundance levels 50% below those in continuous forest by 1997 (Schmiegelow et al. 1997, Schmiegelow and Hannon 1999). Continued monitoring of the population trend of this species at Calling Lake can increase our knowledge of responses to fragmentation effects, which may not emerge within short time frames. Time lags in songbird response to fragmentation, owing to site-

fidelity changes occurring with successive generations (Bellamy et al. 2000), are possible. Also, temporal variation in songbird abundance levels due to natural cycles is more apparent in long-term studies (Collins 2001). While large-scale landscape experiments are logistically difficult to implement, they minimize sources of confounding variation and thus are vital for evaluating underlying processes (Debinski and Holt 2000, McGarigal and Cushman 2002).

1.2 Natural History

The black-throated green warbler is the eastern representative of the *Dendroica virens* superspecies, a complex of insectivorous warblers widespread throughout North America (Curson et al. 1994). It is a Neotropical migrant that winters primarily in Mexico and Central America, and breeds mainly in northeastern North America, yet with a summer range extending to eastern British Columbia and northern Alberta (Morse 2005). Most population-level studies have occurred in the eastern portions of the range, where the species is generally associated with coniferous forest stands (Morse 2005). In contrast, Robichaud and Villard (1999) studied the black-throated green warbler in Alberta, documenting a preference for conifers within deciduous-dominated forests. Another long-term study in northern Alberta found <5% of detections were from stands containing >50% white spruce (F. Schmiegelow, *unpubl. data*). However, there remains a paucity of information on the breeding ecology of this species in the western boreal forest.

Imbeau et al. (2001) note that a songbird's preferred forest successional stage is the most important determinant of a species' response to forest management. Many studies have identified the black-throated green warbler as an interior, old-growth forest

specialist, sensitive to habitat change (Westworth and Telfer 1993, Kirk et al. 1996, Schmiegelow and Hannon 1999), and associated with older mixedwood boreal forest in Alberta (Robichaud and Villard 1999). Projections anticipate a reduction in mixedwood forests, coupled with a truncation of the forest age structure on the landscape, should current forestry practices continue (Hobson and Bayne 2000, Schneider et al. 2003). Thus far, Breeding Bird Surveys suggest no consistent range-wide change in the population since 1966 (Sauer et al. 2005), however whether BBS surveys can accurately detect this species is uncertain (Schmiegelow and Mönkkönen 2002). Nonetheless, habitat loss and population declines in the western portion of its range have warranted listing the black-throated green warbler as a Species at Risk in Alberta (Norton 1999).

1.3 Thesis Overview

The focus of this thesis is to document the pattern and explore the process underlying the decline of the black-throated green warbler originally noted 5 years post-harvest as part of the Calling Lake Fragmentation Experiment (Schmiegelow et al. 1997, Schmiegelow and Hannon 1999). Chapter 2 describes the pattern of the population trend from 1993 through 2004 at Calling Lake, determined from point count surveys conducted as a component of the Calling Lake Fragmentation Experiment. Generalized linear modelling was subsequently used to examine the relative effects of forest structure, spatial structure (patch size and treatment), and an indirect measure of habitat quality (defined by abundance of black-throated green warblers pre-harvest) on predicting patch occupancy over time. The pattern documented in Chapter 2 was examined in Chapter 3 by exploring potential mechanisms contributing to the decline. Multiple factors including area effects and edge effects, the latter represented by vegetation change through time

and edge avoidance, were explored. To fully describe the effects of vegetation change, an analysis of habitat selection at multiple scales was first conducted to identify preferred vegetation attributes whose reduction may have affected the black-throated green warbler population. Habitat quality, defined by territory size, pairing status, and reproductive success, was also compared between the isolated fragments and the continuous control sites. The final chapter of this thesis summarizes the results from Chapters 2 and 3, applying them in a conservation and management framework, and concludes by recommending future research directions to enhance the knowledge base for this species in the western boreal forest.

1.4 Literature Cited

Bellamy, P.E., Rothery, P., Hinsley, S.A. and I. Newton. 2000. Variation in the relationship between numbers of breeding pairs and woodland area for passerines in fragmented habitat. Ecography 23(1): 130-138.

Böhning-Gaese, K., Taper, M.L. and J.H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 7:76-86.

Brotons, L., Thuiller, W., Araujo, M.B., and A.H. Hirzel. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27: 437-448.

Carignan, V. and M.-A. Villard. 2002. Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment 78: 45-61.

Collins, S.L. 2001. Long-term research and the dynamics of bird populations and communities. Auk 118(3): 583-588.

Curson, J., Quinn, D., and D. Beadle. 1994. New World Warblers. Christopher Helm, London. 252 pp.

Debinski, D.M. and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14(2): 342-355.

Donovan, T.M., Thompson III, F.R., Faaborg, F.R. and J.R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9(6): 1380-1395.

Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98(3): 447-458.

Hagan, J.M.III, Vander Haegen, W.M. and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188-202.

Hames, R.S., Rosenberg, K.V., Lowe, J.D., and A.A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. Journal of Animal Ecology 10: 182-190.

Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19(3): 768-782.

Hobson, K.A. and E.M. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. Condor 102(4): 759-769.

Imbeau, L., Mönkkönen, M., and A. Desrochers. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conservation Biology 15(4): 1151-1162.

Kirk, D.A., Diamond, A.W., Hobson, K.A. and A.R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Canadian Journal of Zoology 74: 1749-1770.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, NJ.

McGarigal, K. and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12(2): 335-345.

Morse, D. H. 2005. Black-throated Green Warbler (*Dendroica virens*). *In* The Birds of North America (A. Poole, Ed.). Cornell Laboratory of Ornithology, Ithaca, NY. [online]: http://bna.birds.cornell.edu/BNA/account/Black-throated_Green_Warbler/. (Revised August 2005).

Norton, M.R. 1999. Status of the black-throated green warbler (*Dendroica virens*)

in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 23, Edmonton, AB. 24 pp.

Robbins, C.S., J.R. Sauer, R. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Science (USA) 86: 7658-7662.

Robichaud, I.R. and M.-A. Villard. 1999. Do black-throated green warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101: 262-271.

Robinson, S.K., Thompson, F.R. III, Donovan, T.M., Whitehead, D.R. and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1990.

Sauer, J. R., Hines, J.E., and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966 - 2004. Version 2005.2. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schmiegelow, F.K.A. and S.J. Hannon. 1993. Adaptive management, adaptive science, and the effects of forest fragmentation on boreal birds in northern Alberta. Transactions of the 58th North American Wildlife and Natural Resources Conference: 584-598.

Schmiegelow, F.K.A. and S.J. Hannon. 1999. Forest-level effects of management on boreal songbirds: the Calling Lake fragmentation studies. *In* Forest Fragmentation: wildlife and management implications, pp 201-220. Edited by J.A. Rochelle, L.A. Lehmann and J. Wisniewski. Brill, Boston, MA.

Schmiegelow, F.K.A., Machtans, C.S. and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78(6): 1914-1932.

Schmiegelow, F.K.A. and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12(2): 375-389.

Schneider, R.R., Stelfox, J.B., Boutin, S., and S. Wasel. 2003. Managing the cumulative impacts of land uses in the western Canadian sedimentary basin: a modeling approach. Conservation Ecology 7(1): 8.

Thompson, I.D. 2004. The importance of superior-quality wildlife habitats. Forestry Chronicle 80(1): 75-81.

Westworth, D.A. and E.S. Telfer. 1993. Summer and winter bird populations associated with five age classes of aspen in Alberta. Canadian Journal of Forest Research 23: 1830-1836.

Zanette, L. 2000. Fragment size and the demography of an area-sensitive songbird. Journal of Animal Ecology 69: 458-470.

Chapter 2

DECLINES IN THE BLACK-THROATED GREEN WARBLER: PATTERN

2.1 INTRODUCTION

The boreal forest is recognized as vital for the population persistence of breeding songbirds in North America (Niemi et al. 1998, Blancher 2003). The Canadian boreal forest has recently been targeted for proactive conservation planning, as it is now known to contain almost one quarter of intact forest worldwide (Global Forest Watch Canada 2000). However, boreal forests are changing at an unprecedented rate, driven largely by anthropogenic activities such as forestry, oil and gas exploration, and agricultural expansion, coupled with the additive effects of natural events such as wildfire and insect outbreaks (Hobson et al. 2002, Schneider et al. 2003). These activities contribute to forest fragmentation and habitat loss, which have been implicated in declines of insectivorous songbirds on breeding grounds elsewhere in North America (Böhning-Gaese 1993, Robinson et al. 1995). Forest fragmentation can negatively impact songbirds through area effects, where retained patch size is inadequate for territory and breeding requirements (Bender et al. 1998, Bellamy et al. 2000); isolation effects, when dispersal between isolated fragments and intact forest blocks is limited (Hames et al. 2001); and edge effects, through microclimate or vegetation changes, or through increased nest predation and nest parasitism (Hagan et al. 1996, Flaspohler et al. 2001). Resultant declines are often due to a reduction in habitat quality, defined both by attributes of the forest patch, as well as those of the surrounding matrix (Schmiegelow and Mönkkönen 2002, Brotons et al. 2003). The dynamics of the matrix (i.e. harvested area) in a managed forest system differ from those in agricultural systems, as there is no

permanent conversion to non-forested habitat, but rather forest succession is re-set (Bayne and Hobson 1997, Ibarzabal and Desrochers 2001). As the matrix habitat regenerates following harvest, edge effects diminish as the patch contrast decreases (Harper and MacDonald 2002). As well, the effects of fragment isolation may diminish over time with matrix regeneration (Brotons et al. 2003).

Habitat quality should be measured by individual fitness, i.e. an organism's ability to produce offspring, rather than by density (Van Horne 1983, Vickery et al. 1993), however it may not be feasible to conduct population-level surveys for species of conservation concern. High quality habitat can be coarsely identified by mapping songbird distribution patterns and habitat associations (Sergio and Newton 2003, Thompson 2004). These patterns can then be used to narrow the focus of research towards specific fine-scale questions aimed at identifying underlying mechanisms, and can aid in predicting species' occurrence in order to meet management objectives. Ideally, indicator species that respond to ecosystem changes can be identified and monitored to detail causal relationships that can be incorporated into an adaptive management framework to ensure sustainability of the boreal forest (Venier and Pearce 2004). Birds can be used as indicators of ecosystem condition, as they utilize both functional and structural aspects of their habitat (Furness and Greenwood 1993, Niemi et al. 1998). Certain songbirds are more sensitive to landscape change and can be used as indicators to monitor land use impacts over time (Hausner et al. 2003). The black-throated green warbler (*Dendroica virens*) is considered an interior forest specialist, requiring older mixedwood habitat for breeding in the western boreal forest (Schieck and Nietfeld 1995, Kirk et al. 1996). It has been identified as a species at high risk of

population declines due to the effects of forest fragmentation and projected declines of suitable habitat (Morse 1993, Schmiegelow and Hannon 1993, Schmiegelow and Hannon 1999). The black-throated green warbler experienced declines of ~50% in experimental forest fragments relative to control sites, five years post-harvest in the Calling Lake Fragmentation Experiment in Alberta (Schmiegelow and Hannon 1999). The species has been recognized as a 'Species of Special Concern' in the province of Alberta due to the rate of loss of breeding habitat currently occurring in the western boreal forest (Norton 1999).

The Calling Lake Fragmentation Experiment, initiated to determine the effects of forest fragmentation on the songbird community (Schmiegelow and Hannon 1993), allows for an evaluation of the relative influence of three determinants on occupancy. The design of the experiment includes both a treatment effect, comparing isolated forest fragments to continuous control forests, as well as varying site sizes, to examine the effect of patch size. This design, when coupled with an assessment of habitat associations and pre-harvest abundance data to describe habitat quality, allows for a coarse-scale evaluation of the relative effects of spatial structure, forest structure, and habitat quality on occupancy patterns of black-throated green warblers post-harvest.

This chapter has two main objectives: first, to analyze the 12-year population trend of black-throated green warblers in the forest fragments and control forests of the Calling Lake Fragmentation Experiment to examine broad-scale treatment effects. I predicted that over time the effects of fragmentation would decrease as the edge contrast softened and isolation was diminished with matrix regeneration, leading to an increase in the abundance of black-throated green warblers in the fragments, or apparent recovery

relative to control sites. The second objective of this chapter is to model the pattern of local occupancy to determine which variables predict black-throated green warbler occurrence: habitat quality, forest structure, spatial structure, or a combination of these. As black-throated green warblers are habitat specialists, sensitive to habitat change, and exhibit site-fidelity (Morse 2005), I expected that all 3 determinants in concert would be necessary to predict black-throated green warbler patch occupancy over time.

2.2 METHODS

2.2.1 Study Area

This study was conducted in the mixedwood boreal forest of north-central Alberta, near Calling Lake (55° 13' N, 113° 19' W). The study area is approximately 250 km north of Edmonton, and encompasses ~14,000 ha (Figure 2.1). Upland sites consist of an overstory dominated by trembling aspen, (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*). Mid-layer species include alder (*Alnus crispa* and *A. tenufolia*) and paper birch (*Betula papyrifera*), with a shrub layer of rose (*Rosa* spp.), raspberry (*Rubus idaeus*), cranberry (*Viburnum* spp.), and honeysuckle (*Lonicera* spp.). Both pure and mixedwood stands exist. Historically, stand initiation was predominately due to wildfires, with moderate to smaller scale disturbances such as insect outbreaks and gap dynamics contributing to a patchy landscape mosaic.

2.2.2 Experimental Design

Study sites were established in 1992 as part of the Calling Lake Fragmentation Experiment (see Schmiegelow and Hannon 1993). At that time, the area was relatively pristine with little to no industrial development. In the winter of 1993/94, the area was

experimentally harvested to examine the effects of forest fragmentation on boreal songbirds (Schmiegelow et al. 1997). Forest fragments of four sizes (1, 10, 40, and 100 ha), each replicated 3 times, were isolated by a minimum 200-m wide cutblock. Matching control sites were established in continuous, unharvested forest of the same age and composition (Fig. 2.2). Connected fragments of 1, 10, and 40-ha were also established, isolated by cutblocks on 3 sides, but linked to continuous forest on the fourth side by a 100-m riparian buffer strip (Hannon and Schmiegelow 2002). Data from the 1-ha sites and from the connected fragments were not used in this study, as these sites supported few black-throated green warblers, and as examination of the greatest contrast possible required inclusion of 100-ha sites, which were not represented by the connected fragments. All sites were located in deciduous-dominated mixedwood forest, in older stands ranging from 90-140 years of age. Residuals were left in the harvested areas according to deciduous cutblock standards at the time, with 8 standing live or dead trees per hectare for wildlife habitat (Alberta Environmental Protection 1994*a*). No post-harvest site treatment occurred.

Point count stations (100-m radius) were systematically located in a 200-m grid within each site. Number of point count stations per site was proportional to area: 10, 40, and 100-ha site contained 2, 8, and 20 point count stations, respectively. Thus 180 point count stations (90 in the control sites, 90 in the fragment sites), distributed within 900 ha of sampling sites, throughout 140 km^2 of study area (Figure 2.2), were included in this study.

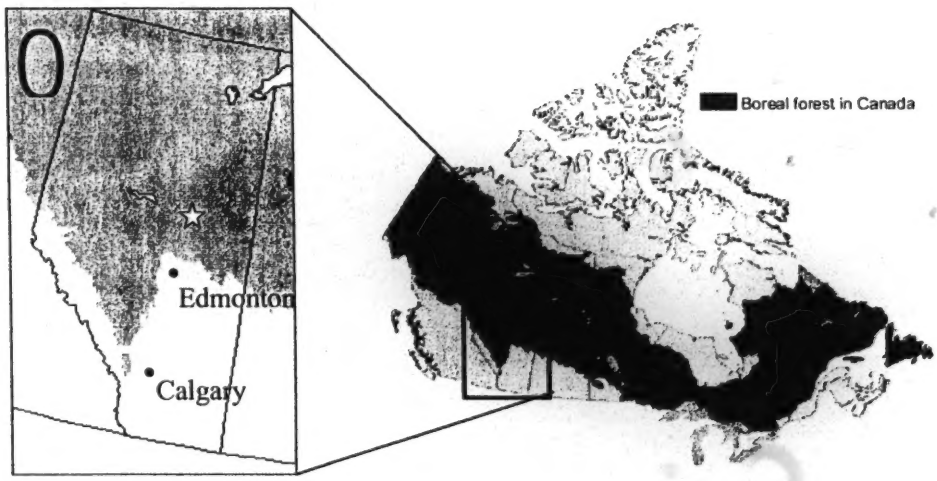

Figure 2.1 Location of the Calling Lake Fragmentation Experiment study area, in Canada and Alberta, denoted by the star.

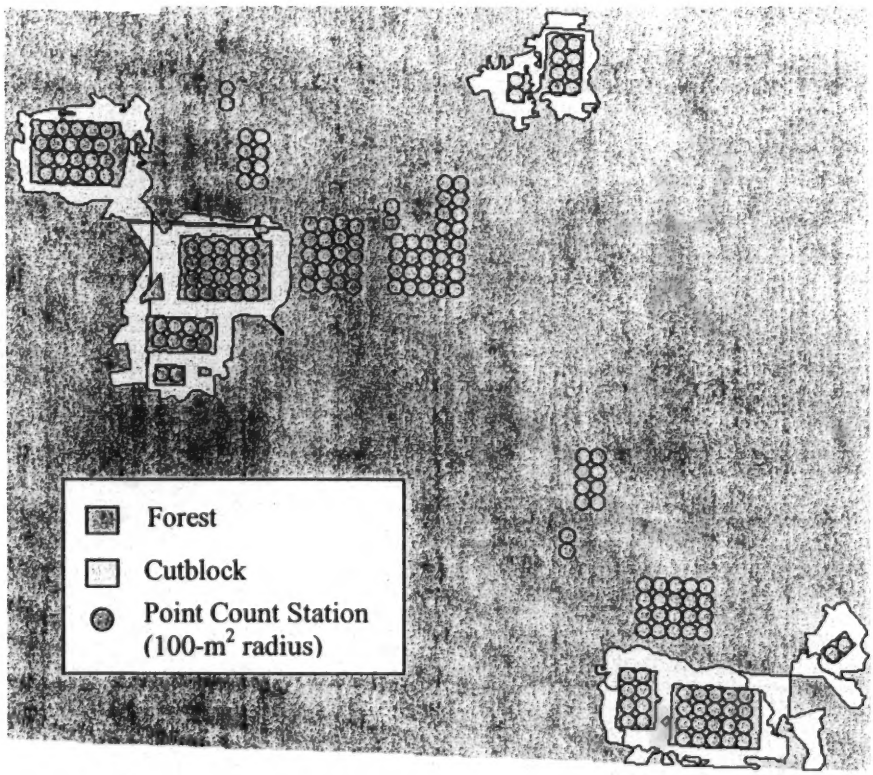

Figure 2.2 Spatial layout of the point count stations (n=180) within the Calling Lake Fragmentation Experiment study area; fragment sites are isolated by cutblocks (white) and control sites are embedded within a continuous forest matrix (grey).

2.2.3 Point Counts

Point count surveys were conducted from 1993 (pre-harvest) through 2004. Five-minute, 100-m fixed radius point counts (Ralph et al. 1995) were conducted from dawn to 5-hours post-dawn, with 5 visits per station spaced 10 days apart from May 17-July 1. All bird species detected passively by sight and sound were recorded, as was behaviour and sex where identified (Bibby et al. 1992). Observers reduced double-counting of individuals by mapping bird movements within and between stations, and by recording counter-singing behaviours. While number of observers varied between years, observers and start locations were rotated every visit, and sampling intervals were consistent between years, to reduce observer and temporal biases. Weather conditions were similar across all sampling bouts, with no surveys conducted in inclement weather (rain and/or high wind). The first visit in each year was excluded from all analyses, as black-throated green warblers were still arriving, leaving 4 visits/year to each station, from May 27 - July 1.

Black-throated green warblers have a characteristic, easily detected voice with 2 different song types (Morse 1967, 1970). Males sing from high in the canopy (T.Hannah, *pers. obs.)* and are infrequently detected visually; females are quite secretive, and are rarely seen or heard (Robichaud and Villard 1999, Morse 2005). Detections on point counts were thus primarily of singing males. Detections of singing males may represent non-territorial floaters attempting to attract females (Hensley and Cope 1951, Van Horne 1983, Sherry and Holmes 1989, Newton 1998). However, visiting sites multiple times within a breeding season, a minimum of 10 days apart, and calculating average abundance rather than maximum abundance, favours identification of territorial males

(Bibby et al. 1992). While maximum abundance is a better measure of true abundance (Toms et al. *in press*), average abundance is the most accurate representation of actual reproductive activity for most forest songbirds (Betts et al. 2005).

2.2.4 Statistical Analyses

2.2.4.1 Population trend

Numbers of black-throated green warblers at each point count station were summed across visits within a breeding season, and divided by the number of visits, to yield an average abundance per station per year. These data were averaged for each treatment type for each year to generate population trends for the control sites and fragment sites. A repeated measures analysis of variance with contrasts was performed to test for annual differences between treatments, i.e. to test specifically for a year x treatment interaction. Contrasts between annual abundance and pre-harvest abundance were used to account for pre-harvest variation in abundance levels between fragment and control sites. A Mann-Whitney non-parametric analysis was performed to test for pre-harvest differences, as the 1993 data did not follow a normal distribution (Zar 1999). SPSS 13.0 (2004) was used for these analyses. Means are presented ± one standard deviation. Differences were considered significant at $\alpha = 0.10$, to minimize Type II errors, which are of concern in conservation-related research (Smith 1995).

2.2.4.2 Patch occupancy

Annual abundance values at a point count station were converted into a binomial variable: occupied (0) or not occupied (1), where an average abundance value of 0.5 was used as a cut-off to determine occupancy. This cut-off ensured only territorial detections

were included, defined as a minimum of 2 registrations, ≥10 days apart (Robbins 1970). The number of occupied years from 1994-2004 was summed to produce a response variable for each point count station, signifying number of years occupied post-harvest. As black-throated green warbler territories are approximately the same size as a point count station (see Section 3.3.3), predictions on occupancy modelled at the point count station-level relate to territory occupancy, hereafter referred to as 'patch'.

Five independent variables were generated to evaluate three hypotheses related to patch occupancy: forest structure, spatial structure and habitat quality (Table 2.1). For each point count station, the 1993 abundance was determined by calculating the average abundance ('cnt93'), which is referred to as the 'habitat quality' metric as it relates to pre-treatment abundance levels. Two spatial structure descriptors were assigned to each station: treatment type (control or fragment) and size (categorical: a = 10-ha, b = 40-ha, c = 100-ha). Percentages of vegetation composition and structure obtained from Alberta Vegetation Inventory data, were weighted by area for each stand within a point count station to develop habitat metrics using ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA) with the Xtools extension (DeLaune 2003). The Alberta Vegetation Inventory (Nesby 1997) is a digital data layer interpreted from 1:20 000 aerial photographs. Stand boundaries are delineated with 20-m accuracy, stand origin is derived from overstory height and tree coring , and species composition is assigned to each stand in increments of 10% (Alberta Environmental Protection 1994*b*). The digital layer was updated in 2001/2002, and projected in NAD27 Zone 12. Using these data, 3 area-weighted metrics were calculated for each point count station describing forest structure; percent white spruce in the overstory (sw), stand age (age), and stand height

(hgt). Colinearity between independent variables was examined using Pearson's correlations. Stand age and stand height were significantly correlated (correlation coefficient = |0.91|), thus stand height was dropped from all analyses. The stand age variable was selected for retention as it is more likely to be used for management planning than stand height (G. Dribnenki, *pers. comm.*). Colinearity was not present between any other independent variables based on the selected cut-off value of >|0.5|.

Table 2.1 Independent variables used in a generalized linear model describing occupancy of point count stations by black-throated green warblers from 1994-2004; dependent variable is 'number of years occupied'.

Inference	Variable	Description	Data type
Habitat Quality	cnt93	Average abundance of birds/station in 1993 (pre-harvest)	Continuous
Forest Structure	sw	Area-weighted percent white spruce	Continuous
	age	Area-weighted stand age	Continuous
Spatial Structure	treat	Treatment: Fragment or Control	Categorical
	size	Site size: a (10 ha); b (40 ha); c (100 ha)	Categorical

Generalized linear modelling to predict patch occupancy was performed assuming a negative binomial distribution in S-plus 6.2 (2003). The multiple-working hypotheses method of model selection was used (Anderson et al. 2000), where candidate models are compared using Akaike Information Criteria corrected for small sample sizes (AIC_c) (sample size divided by the number of parameters is < 40; Burnham and Anderson 2002). The model with the lowest AIC_c value explains the greatest variation with the fewest variables, and if candidate models are < 2 AIC_c units apart they are equally well supported (Burnham and Anderson 2002). This technique combines the concept of maximizing model fit with the idea of parsimony, in order to select the best model from the subset (Johnson and Omland 2004).

A total of 12 candidate models were compared. Each model was specified *a priori* based on biologically-relevant predictions, which combined aspects of the three potential determinants: spatial structure, forest structure, and habitat quality. Data were initially evaluated graphically for non-linear relationships, which were suggested for two of the independent variables, 'sw' and 'age'. Based on scatterplots and an initial spline fit, non-linear functions were incorporated into candidate models to determine if adding a non-linear function aided in explaining variation in the response variable (Crawley 2002). Non-linear terms added to the model included a 2nd order polynomial function for 'age' and a log transformation of 'sw'. The models were ranked based on the difference between AIC_c values and the minimum value (AIC_{ci} - minAIC_c) and an Akaike weight (w_i) was assigned to each describing the relative amount of support for the model from amongst the set considered (Johnson and Omland 2004). The number of parameters, K, was calculated for each model as the sum of all independent variables plus 2 (one for the intercept and one for the random error term) as required for models estimating maximum likelihoods (Burnham and Anderson 2002).

2.3 Results

2.3.1 Population Trend

A total of 180 point count stations (controls, n=90; fragments, n=90) were surveyed from 1993-2004 to document the population trend. Pre-harvest abundance levels (1993) did not differ between controls and fragments (Mann-Whitney U= 3938.0, p=0.74). Average abundance at a point count station across the post-harvest time frame (1994-2004) was 0.31± 0.13 in controls and 0.22 ± 0.11 in fragments. Results of the repeated measures analysis of variance revealed a significant difference in abundance

between fragments and controls, relative to 1993, in 1994 and in 1997-2001, inclusive (Figure 2.3). Of these, 1994 is the only year where fragment abundance was higher than in the controls; all other years had control levels higher than fragment levels (Table 2.2). Commencing in 1998, the controls exhibited a decline, whereas the fragments maintained relatively stable reduced levels. There was no significant difference between abundance levels in controls and fragments in the last 3 years of sampling, suggesting a convergence in abundance levels. By 2004, mean abundance per station across all sites in the study area was 69.4% below pre-harvest levels (from 0.476 individuals in 1993 to 0.146 individuals in 2004).

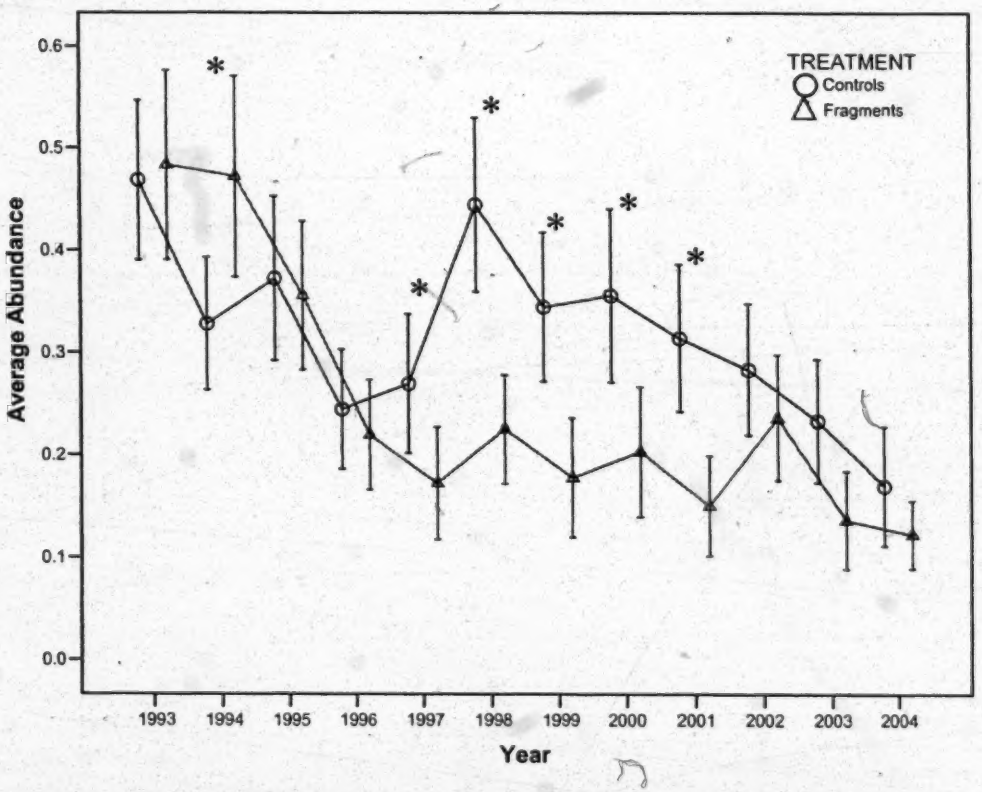

Figure 2.3 Population trend of black-throated green warblers in Fragment sites and Control sites from 1993-2004. Data represent annual average abundance from point counts summed by treatment. Asterisks denote significance at $\alpha = 0.10$ from a repeated measures analysis of variance with contrasts; error bars denote 90% confidence intervals.

Table 2.2 Results from Repeated Measures ANOVA, with contrasts relative to pre-harvest abundance levels. Bold font denotes a significant difference at $\alpha = 0.10$ between abundance of black-throated green warblers in fragments and controls in each year compared to the difference that existed in 1993 (pre-harvest). The sign of difference denotes whether fragment levels are higher (+), lower (-), or not significantly different (nd) in relation to control levels.

Year *vs.* 1993	p-value	Sign of Difference
1994	**0.045**	+
1995	0.76	Nd
1996	0.52	Nd
1997	**0.080**	-
1998	**0.0010**	-
1999	**0.016**	-
2000	**0.013**	-
2001	**0.013**	-
2002	0.36	Nd
2003	0.12	Nd
2004	0.41	Nd

2.3.2 Patch Occupancy

Across a total of 180 point count stations sampled from 1994-2004, number of years occupied ranged from 0 to 11 ($\bar{x}$ =3.1 ± 3.3). Area-weighted white spruce per point count station ranged from 0-35% ($\bar{x}$ = 6.5 ± 7.4), while area-weighted stand age averaged 107.0 ± 16.6 years, with a range of 63-135 years. The mean number of birds detected at the point count station pre-harvest ('cnt93') ranged from 0.0 to 2.0 ($\bar{x}$ = 0.48 ± 0.49).

The top AIC_c model relating to patch occupancy included the following terms: cnt93, a 2nd order polynomial of stand age, and a log transformation of % sw (AIC_c weight = 0.92, Table 2.3). Partial residual plots of these 3 variables are shown in Figure 2.4. The log transform of 'sw' indicates that patch occupancy increased as percentage white spruce increased to ~10%, yet occupancy appeared to plateau above ~10% white spruce. A 2nd order polynomial function of 'age' suggests that patch occupancy was

highest above a stand age of approximately 100 years. 'Cnt93' is a linear function, meaning higher numbers of black-throated green warblers at a station pre-harvest contributed to higher patch occupancy post-harvest. This top-ranked model is 11.5 times more likely to be the best model compared to the next ranked model (evidence ratio = 0.92/0.08), suggesting a large amount of confidence in the top model. Residual deviance explained was 45.8%.

The second-ranked model included similar parameters relating to forest structure and habitat quality, but also included the categorical spatial structure variables of treatment, site size, and the interaction between treatment and site size (AIC_c weight = 0.08). There was a larger gap in AIC_c between the second and third model (ΔAIC_c = 20.84) and there was little to no support for models 3-12 (AIC_c weights of<0.001). The parameters 'log(sw)' and the 2nd order polynomial of 'age' were included in the top 3 models, whereas the categorical 'treat' and 'size' parameters were not in the top model, but appeared in 2 of the top 6 ranked models. The 'cnt93' parameter appeared in 5 of the top 7 competing candidate models, including the top 2 models. As the top two models were separated by an AIC_c difference >2 (ΔAIC_c = 4.92), model averaging to generate estimates of coefficients was not warranted. Coefficients with associated standard errors and 90% confidence intervals from the top model are shown in Table 2.4.

2.4 Discussion

2.4.1 Population trend

Five years post-harvest in the boreal mixedwood forest of northern Alberta, black-throated green warblers had experienced a decline of 50% in experimentally created forest fragments, compared to levels in control forests (Schmiegelow and Hannon 1999).

Table 2.3 Candidate models describing 'number of years occupied' by black-throated green warblers at the point count station level. *K* specifies the number of parameters in the model, ΔAIC_c indicates the change in value between each model and the model with the lowest AIC_c, and w_i is a weight assigned to the model as a relative likelihood that the model is the best amongst those tested.

Rank	Model	*K*	ΔAIC_c	w_i
1	cnt93+log(sw)+age+age^2	6	0.00	0.92
2	cnt93+log(sw)+age+age^2+treat+size+treat*size	11	4.92	0.08
3	log(sw)+age+age^2	5	25.76	<0.001
4	cnt93+sw+age+treat+size+treat*size	10	29.78	<0.001
5	age+age^2	3	50.45	<0.001
6	cnt93	3	81.43	<0.001
7	cnt93+treat+size+treat*size	8	83.42	<0.001
8	log(sw)	3	101.82	<0.001
9	treat	3	137.56	<0.001
10	null	2	137.99	<0.001
11	treat+size+treat*size	7	140.00	<0.001
12	size	4	140.46	<0.001

Table 2.4 Coefficients, standard errors, and 90% confidence intervals for the terms in the top ranked model describing black-throated green warbler occupancy at Calling Lake point count stations from 1994-2004.

Variable	β	SE	90% C.I.	
			Lower	Upper
Intercept	-18.73	4.17	-25.91	-12.04
cnt93	0.71	0.12	0.50	0.92
age	0.34	0.075	0.22	0.47
age^2	-0.0014	0.00034	-0.0020	-0.00084
log(sw)	0.31	0.059	0.22	0.41

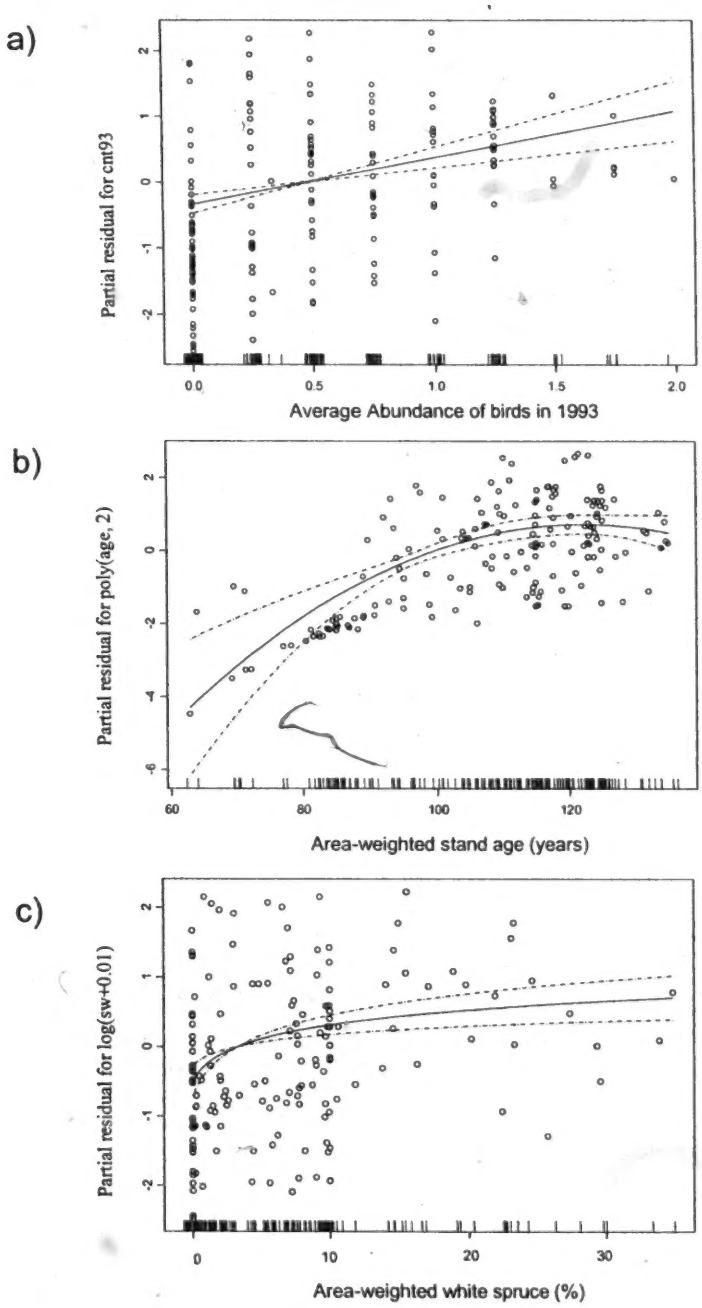

Figure 2.4 Partial residual plots of parameters included in the top generalized linear model describing occupancy of black-throated green warblers at point count stations from 1994-2004 in the Calling Lake Fragmentation Experiment; a = average abundance of birds per station in 1993, pre-harvest; b = 2nd order polynomial of area-weighted stand age; c = log transformed area-weighted percent of white spruce in the overstory.

An initial crowding effect (Hagan et al. 1996) was followed by a reduction in density in isolated patches, as predicted by island biogeography theory (MacArthur and Wilson 1967). Continued documentation of the population trend through to 2004 revealed a convergence between the abundance levels in the isolated fragments and continuous control sites. I predicted such a convergence would occur over time as the effects of fragmentation diminished with regeneration of the matrix surrounding the fragments. However, the convergence detected between the two population trends was not due to a recovery of abundance in the fragments, but rather a decrease in the abundance of black-throated green warblers in the control forests, with the fragments maintaining a reduced abundance level. Moreover, the total population in the study area in 2004 (fragments and controls combined) was almost 70% below the levels measured in 1993. As this study was designed as an experiment to test the effects of forest fragmentation, there was an attempt to minimize all internal sources of variation, such that forest structure and stand age was standardized between fragments and controls (Schmiegelow and Hannon 1993). The population decline documented in the controls is therefore surprising, suggesting potential regional factors for the decline. However, I focus here on the local determinants of distribution and abundance that I directly evaluated.

2.4.2 Patch Occupancy

Of the 3 potential determinants of black-throated green warbler patch occupancy, spatial structure, forest structure, and habitat quality, only the latter 2 factors were included in the model best predicting occupancy post-harvest. Maximum patch occupancy occurred consistently at a stand age of ~100-130 years and ~5% or more white spruce in the overstory, consistent with previous descriptions of habitat associations for

this species (Kirk et al. 1996, Norton 1999, Robichaud and Villard 1999, Morse 2005). Terms describing spatial structure as part of the Calling Lake Fragmentation Experiment (i.e. treatment and site size) did not contribute significantly to describing variation in patch occupancy, contrary to my prediction. This is most likely due to the decline experienced in the control sites, which confounded the interpretation of the treatment effect. Potential contributors to this decline are discussed later in this section.

The term describing abundance in 1993 was not statistically correlated with forest structure attributes in the model, yet was included in many of the top models predicting patch occupancy post-harvest. Bird settlement is driven by the need to select high quality habitat (Sergio and Newton 2003). Knowledge of high quality sites stems from numerous sources, including direct experience, as well as intra-, and inter-specific interactions. Adults exhibit site-fidelity, returning to successful, high quality territories in subsequent years (Boulinier and Danchin 1997, Switzer 1997, Schmidt 2004). Migrants also cue-in to resident species, which are often found in higher quality habitat (Thomson et al. 2003). As well, individuals exploit intraspecific attraction, as the abundance and/or distribution of conspecifics in neighbouring patches may be a predictor of higher quality habitat and results in more effective territorial defence, predator protection, and mate attraction (Stamps 1988, Muller et al. 1997). Baseline survey data to some extent incorporate these behaviour-based settlement decisions in recorded patterns of distribution, and are essential to being able to effectively monitor the effects of anthropogenic change on biological systems.

Forest structure was a predictor of post-harvest patch occupancy, with both percent white spruce and stand age included in the top model, based on coarse-scale

metrics derived from the Alberta Vegetation Inventory. It is possible these coarse-scale metrics are also indicators of fine-scale attributes necessary for black-throated green warbler persistence. Older forests with low levels of white spruce in the overstory represent multi-layered, structurally diverse habitat, often containing canopy gaps created by natural small-scale disturbances (Bersier and Meyer 1994, Kirk et al. 1996, Cumming et al. 2000). Smith and Dallman (1996) have shown that black-throated green warblers used forest gaps significantly more than expected compared to contiguous forests in Michigan. These gaps have increased light penetration, which may increase prey activity and abundance, and may aid avian thermodynamics as warmer temperatures reduce thermoregulatory costs (Smith and Dallman 1996). As well, vegetative structure in gaps may assist territory defence by increasing visibility and song projection (Smith and Dallman 1996). Collins (1983) found that black-throated green warblers were associated with a range of habitats throughout the north-eastern United States that varied significantly in both vegetation composition and structure. Further examination of occurrence and behaviour patterns could help explain finer-scale selection patterns in the western boreal forest.

Coarse-scale and stand-level patterns of black-throated green warbler distribution appear to be successful in identifying areas of high occupancy, yet this does not necessarily imply successful breeding (Vickery et al. 1993). Without associated measures of habitat-specific fitness, there is a risk that long-term population persistence may not be achieved, even with maintenance of apparently selected habitats. It is necessary to identify finer-scale habitat selection, measure fitness, and document behavioural responses to landscape change, such as edge avoidance and territory size

changes. While observed patterns can focus future research, understanding the underlying processes is necessary to achieve effective conservation and management.

2.4.3 Broader Determinants of the Local Decline

Many potential causes have been suggested for the decline in migratory songbirds documented over the past few decades. These range from drought (Blake et al. 1989), disease (Rappole and Hubálek 2003), habitat loss on the wintering or breeding grounds (Terborgh 1989, Rappole and McDonald 1994), and increased nest parasitism (Brittingham and Temple 1983) or nest predation (Böhning-Gaese et al. 1993) associated with habitat fragmentation (Hagan et al. 1996). The latter two factors were explored at Calling Lake in the first few years following fragmentation, and it was determined that neither nest predation nor nest parasitism had significantly increased in fragments relative to interior forest (Cotterill and Hannon 1999, Song and Hannon 1999, S.J. Hannon and M.-A. Villard *unpubl. data*). It is possible disease and wintering-ground effects are causing the decline, yet the lack of an observed decline in the range-wide population of black-throated green warblers suggests it is a more local phenomena.

In the past decade, oil and gas exploration and development in Alberta has increased dramatically. While every attempt was made to curtail the amount of activity in the study area, some linear features were established within study sites resulting in direct habitat loss. However, this loss was not equivalent to the scale of the observed decline, i.e. the cutlines did not remove 70% of the habitat from within the sites. The cutlines may have behavioural implications, as other studies have documented effects on gap-crossing by forest birds at widths as low as 25-m (Rail et al. 1997, Bélisle and Desrochers 2002). Nevertheless, observations of black-throated green warblers crossing

50-m wide pipelines, as well as leaving fragment sites (i.e. crossing >150-m wide gaps) were noted in the Calling Lake study area in both 2003 and 2004 (T. Hannah, *pers. obs.)*. In a test of gap-sensitivity, black-throated green warblers demonstrated only a slight benefit from the presence of narrow forest corridors, and this benefit was temporally inconsistent (Hannon and Schmiegelow 2002). It remains unclear whether unplanned modifications to the study area affected bird behaviour, and consequently abundance. Potential effects should be further explored.

Threshold responses to amount of cover have been documented in many forest songbirds (e.g., Villard et al. 1999, Guénette and Villard 2005, Suorsa et al. 2005, Watson et al. 2005), but have yet to be evaluated for black-throated green warblers in the western boreal forest. It is possible that this species exhibits sensitivity to the amount of forest cover present at a regional scale, and that with escalating forest harvest over the past decade, thresholds have been surpassed, affecting the population at Calling Lake. While BBS data suggest no long-term decline, the paucity of routes through the northern boreal forest, coupled with the difficulty in detecting interior forest songbirds from roadside surveys (Schmiegelow and Mönkkönen 2002), suggest that these data are inadequate for detecting long-term declines of this species. Larger-scale controls and replication across regions would aid in removing confounding sources of variation that mask true treatment effects (McGarigal and Cushman 2002, Fahrig 2003, Parker et al. 2005).

2.4.4 Conservation and Management Implications

The overall decline experienced by black-throated green warblers at Calling Lake from 1993-2004 is almost 70%. This species has been recognized as a species at risk in

the province of Alberta, yet no measures have been put in place to ensure continued population monitoring and habitat protection. Additional demographic studies, and a biomonitoring program to track population trends for adaptive management purposes, would support conservation and management of black-throated green warbler populations in the western boreal forest. Research focusing on fitness attributes, prey availability, and dispersal would be useful in clarifying some of the patterns documented here. Whether the overall decline observed in the population at Calling Lake is a local, regional, or wintering-ground phenomenon should be further explored

Current forestry practices in Alberta target older forests for harvest, using a 2-pass clearcut system, where the second harvest occurs in adjacent forest ~10 years after the first harvest, within a 70- year rotation cycle (Schneider et al. 2003). This harvest system will lead to a substantial reduction of black-throated green warbler habitat in the boreal forest of Alberta, with older forests existing primarily in riparian buffer areas, inaccessible locales, and in isolated reserve patches (Hannon and Schmiegelow 2002). This species also requires a minimum percentage of white spruce in the overstory of mixedwood forests; these stands are at risk due to existing harvesting techniques which convert mixedwood forests into single-species managed stands (Hobson and Bayne 2000). Maintaining older (at least 100-years), mixedwood forest stands on the landscape is necessary for regional population persistence of the black-throated green warbler. Determining the amount and spatial distribution of this forest type necessary to support populations over the long-term (i.e. multiple forest rotations) is a significant research challenge.

2.5 Literature Cited

Alberta Environmental Protection. 1994*a*. Alberta timber harvest planning and operating ground rules. Natural Resources Service, Recreation and Protected Areas Division. Edmonton, AB.

Alberta Environmental Protection. 1994*b*. Alberta vegetation inventory standards manual, Version 2. Land Information Division, Resource Information Development Branch. Edmonton, AB.

Anderson, D.R., Burnham, K.P. and W.L. Thompson. 2000. Null hypothesis testing: Problems, prevalence and an alternative. Journal of Wildlife Management 64(4): 912-923.

Bayne, E.M. and K.A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation on artificial nests. Conservation Biology 1(6): 1418-1429.

Bélisle, M. and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17: 219-231.

Bellamy, P.E., Rothery, P., Hinsley, S.A. and I. Newton. 2000. Variation in the relationship between numbers of breeding pairs and woodland area for passerines in fragmented habitat. Ecography 23(1): 130-138.

Bender, D.J., Contreras, T.A., and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79(2): 517-533.

Bersier, L.F., and D.R. Meyer. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecologica 15: 561–576.

Betts, M.G., Simon, N.P.P. and J.J. Nocera. 2005. Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. Journal of Ornithology 146: 151-159.

Bibby C.J., Burgess, N.D. and D.A. Hill. 1992. Bird Census Techniques. British Trust for Ornithology and Royal Society for the Protection of Birds and Academic Press. San Diego, CA.

Blake, J.G., Niemi, G.J. and J.M. Hanowski. 1989. Drought and annual variation in bird populations. Pp. 419-430 *in* Ecology and conservation of neotropical migrant landbirds (J.M. Hagan III and D.W. Johnston, Eds.) Smithsonian Institution Press, Washington, D.C.

Blancher, P. 2003. Importance of Canada's boreal forest to landbirds. Canadian Boreal Initiative and Boreal Songbird Initiative. 40 pp.

Böhning-Gaese, K., Taper, M.L., and J.H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 7:76-86.

Boulinier, T. and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. Evolutionary Ecology 11(5): 505-517.

Brittingham, M.C., and S.A. Temple. 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33(1): 31-35.

Brotons, L., Mönkkönen, M., and J.L. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. American Naturalist 162(3): 343-357.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, a practical information-theoretic approach. Second edition. Springer, New York.

Collins, S.L. 1983. Geographic variation in habitat structure of the Black-throated Green warbler (*Dendroica virens*). Auk 100: 382-389.

Cotterill, S.E. and S.J. Hannon. 1999. No evidence of short-term effects of clear-cutting on artificial nest predation in boreal mixedwood forests. Canadian Journal of Forest Research 29: 1900-1910.

Crawley, M.J. 2002. Statistical Computing: and introduction to data analysis using S-Plus. John Wiley & Sons, Ltd. Chichester, UK.

Cumming, S.G., Schmiegelow, F.K.A., and P.J. Burton. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecological Applications 10(3): 744-759.

DeLaune, M.G. 2003. Xtools ArcView Extension version 15/09/03 [computer program]. Oregon Department of Forestry, Salem, OR.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34: 487-515.

Flaspohler, D.J., Temple, S.A. and R.N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications 11(1): 32-46.

Furness, R.W., and J.J.D. Greenwood, editors. 1993. Birds as monitors of environmental change. Chapman and Hall, London, UK.

Global Forest Watch Canada. 2000. Canada's forests at a crossroads: an assessment in the year 2000. World Resources Institute, Washington, D.C.

Guénette, J.-S. and M.-A. Villard. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. Conservation Biology 19(4): 1168-1180.

Hagan, J.M., Vander Haegen, W.M., and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10(1): 188-202.

Hames, R.S., Rosenberg, K.V., Lowe, J.D., and A.A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. Journal of Animal Ecology 10: 182-190.

Hannon, S.J. and F.K.A. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. Ecological Applications 12 (5): 1457-1468.

Harper, K.A. and S.E. Macdonald. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. Journal of Vegetation Science 13(4): 535-546.

Hausner, V.H., Yoccoz, N.G. and R.A. Ims. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. Ecological Applications 13(4): 999-1012.

Hensley, M.M. and J.B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk: 68(4): 483-493

Hobson, K.A. and E.M. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. Condor 102(4): 759-769.

Hobson K.A., Bayne E.M., and S.L. Van Wilgenburg. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. Conservation Biology 16 (6): 1530-1541.

Ibarzabal, J., and A. Desrochers. 2001. Lack of relationship between forest edge proximity and nest predator activity in an eastern Canadian boreal forest. Canadian Journal of Forest Research 31:117-122.

Johnson, J.B. and K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19(2): 101-108.

Kirk, D.A., Diamond, A. W., Hobson, K.A., and A.R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Canadian Journal of Zoology 74: 1749-1770.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, NJ.

McGarigal, K. and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12(2): 335-345.

Morse, D.H. 1967. The contexts of songs in the Black-throated green and Blackburnian warblers. Wilson Bulletin 79: 62-72.

Morse, D.H. 1970. Territorial and courtship songs of birds. Nature 226:659-661.

Morse, D.H. 1993. Black-throated green warbler (*Dendroica virens*). *In* The Birds of North America, No. 55 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, D.C.

Morse, D. H. 2005. Black-throated Green Warbler (*Dendroica virens*). *In* The Birds of North America (A. Poole, Ed.). Cornell Laboratory of Ornithology, Ithaca, NY. [online]: http://bna.birds.cornell.edu/BNA/account/Black-throated_Green_Warbler/. (Revised August 2005).

Muller, K.L., Stamps, J.A., Krishnan, V.V., and N.H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). The American Naturalist 150(5): 650-661.

Nesby, R. 1997. Alberta vegetation inventory standards manual. Version 2.2. Alberta Environmental Protection. Edmonton, AB. 42 pp.

Newton, I. 1998. Population limitation in birds. London: Academic Press.

Niemi, G., Hanowski, J., Helle, P., Howe, R., Mönkkönen, M., Venier, L. and D. Welsh. 1998. Ecological sustainability of birds in boreal forests. Conservation Ecology [online] **2**(2): 17. URL: http://www.consecol.org/vol2/iss2/art17/

Norton, M.R. 1999. Status of the black-throated green warbler (*Dendroica virens*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 23, Edmonton, AB. 24 pp.

Parker, T.H., Stansberry, B.M., Becker, C.D. and P.S. Gipson. 2005. Edge and area effects on the occurrence of migrant forest songbirds. Conservation Biology 19(4): 1157-1167.

Rail, J.-F., Darveau, M., Desrochers, A. and J. Huot. 1997. Territorial responses of boreal forest birds to habitat gaps. Condor 99(4): 976-980.

Ralph, C., Sauer, J., and S. Droege. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. U.S. Forest Service, Pacific Southwest Research Station. Albany, CA. 187 pp.

Rappole, J.H. and Z. Hubálek. 2003. Migratory birds and West Nile virus. Journal of Applied Microbiology 94(s1): 47-58.

Rappole, J.H. and M.V. McDonald. 1994. Cause and effect in population declines in migratory birds. Auk 111(3): 652-660.

Robbins, C.H. 1970. Recommendations for an international standard for a mapping method for bird census work. Audubon Field Notes 24: 723-726.

Robichaud, I.R. and M.-A. Villard. 1999. Do black-throated green warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101: 262-271.

Robinson, S.K., Thompson, F.R. III, Donovan, T.M., Whitehead, D.R. and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1990.

S-plus 6.2. 2003. [computer program]. Insightful Corporation, Seattle, WA. http://www.insightful.com.

Schieck, J. and M. Nietfeld. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta (J.B. Stelfox, ed.). Alberta Environmental Centre, Vegreville, AB, and Canadian Forest Service, Edmonton, AB, Canada. Pp. 115-158

Schmidt, K.A. 2004. Site fidelity in temporally correlated environments enhances population persistence. Ecology Letters 7: 176-184.

Schmiegelow, F.K.A. and S.J. Hannon. 1993. Adaptive management, adaptive science, and the effects of forest fragmentation on boreal birds in northern Alberta. Transactions of the 58th North American Wildlife and Natural Resources Conference: 584-598.

Schmiegelow, F.K.A. and S.J. Hannon. 1999. Forest-level effects of management on boreal songbirds: the Calling Lake fragmentation studies. *In* Forest fragmentation: wildlife and management implications, pp 201-220. Edited by J.A. Rochelle, L.A. Lehmann and J. Wisniewski. Brill, Boston, MA.

Schmiegelow, F.K.A., Machtans, C.S. and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78: 1914-1932.

Schmiegelow, F.K.A. and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12(2): 375-389.

Schneider, R.R., Stelfox, J.B., Boutin, S., and S. Wasel. 2003. Managing the cumulative impacts of land uses in the western Canadian sedimentary basin: a modeling approach. Conservation Ecology 7(1): 8.

Sergio, F. and I. Newton. 2003. Occupancy as a measure of territory quality. Journal of Animal Ecology 72(5): 857-865.

Sherry, T. W., and R. T. Holmes. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): A removal experiment. Behavioral Ecology and Sociobiology 25: 327–333.

Smith. S.M. 1995. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? Ecology 76(6): 1997-1998.

Smith, R. and M. Dallman. 1996. Forest gap use by breeding Black-throated green warblers. Wilson Bulletin 108(3): 588-591.

Song, S.J. and S.J. Hannon. 1999. Predation in heterogeneous forest: a comparison at natural and anthropogenic edges. Ecoscience 6(4): 521-530.

SPSS for Windows version 13.0. 2004. [computer program]. SPSS Inc., Chicago, IL.

Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. The American Naturalist 131(3): 329-347.

Suorsa, P., Huhta., E., Jantti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V., and H. Hakkarainen. 2005. Thresholds in selection of breeding habitat by the Eurasian treecreeper. Biological Conservation 121: 443-452.

Switzer, P. 1997. Past reproductive success affects future habitat selection. Behavioural Ecology and Sociobiology 40: 307-312.

Terborgh, J. 1989. Where have all the birds gone? Princeton University Press, Princeton, NJ.

Thomson, R.L., Forsman, J.T., and M. Mönkkönen. 2003. Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. Oecologia 134(3): 431-438.

Thompson, I.D. 2004. The importance of superior-quality wildlife habitats. Forestry Chronicle 80(1): 75-81.

Toms, J.D., Schmiegelow, F.K.A., Hannon, S.J. and M.-A. Villard. *In press*. Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? Auk.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Venier, L.A. and J.L. Pearce. 2004. Birds as indicators of sustainable forest management. Forestry Chronicle 80(1): 61-66.

Vickery, P.D., Hunter, M.L., Jr., and J.V. Wells. 1993. Is density an indicator of breeding success? Auk 109(4): 706-710.

Villard, M.A., Trzcinski, M.K., and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13(4): 774-783.

Watson, J.E.M., Whittaker, R.J., and D. Freudenberger. 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? Journal of Biogeography 32(8): 1353-1370.

Zar, J.H. 1999. Biostatistical Analysis. Prentice-Hall, Inc. Upper Saddle River, NJ.

Chapter 3

DECLINES IN THE BLACK-THROATED GREEN WARBLER: PROCESS

3.1 INTRODUCTION

Twelve years of community-level avian surveys conducted as part of the Calling Lake Fragmentation Experiment identified a local decline in the black-throated green warbler population. Mean abundance levels in isolated forest fragments were 50% lower than levels in continuous control forests 5 years post-harvest (Schmiegelow and Hannon 1999); 12 years post-harvest, mean abundance levels between fragments and controls had converged, due primarily to declines of black-throated green warblers in control forests (see Chapter 2). Coarse-scale patterns of occupancy post-harvest (1994-2004) were explained mainly by stand age and stand composition, with only a weak treatment effect (see Chapter 2). The mechanism contributing to the initial decline in the forest fragments remained unknown.

Numerous processes responsible for declines in forest songbirds have been proposed. These include area, edge, and isolation effects, as well as a decrease in habitat quality as a result of fragmentation (e.g. Bender et al. 1998, Schmiegelow and Mönkkönen 2002, Fahrig 2003). Area effects are a consequence of a change in suitable habitat by size, composition, or quality, or from a change in the number of conspecifics (Freemark and Merriam 1986, Hagan et al. 1996). They can also be expressed by thresholds in patch sizes, below which individual occupancy is deterred, or populations are not viable, limiting the use of forest remnants (Zanette 2000). Edge effects, characterized by an increase in predation and/or nest parasitism rates along edges (Flaspholer et al. 2001), reduces the functional area of the patch, restricting use by area-

sensitive species (Villard 1998). Edge effects such as wind and temperature changes that alter the microclimate of the forest interior (Chen et al. 1993) can penetrate up to 100-m into the forest patch (Harper et al. 2005). Microclimate changes can affect both habitat structure and prey availability, which have been identified as important factors influencing fecundity (Zanette et al. 2000, Nagy and Holmes 2004) and territory size (Marshall and Cooper 2004) for insectivorous songbirds.

Patch isolation can also occur through a variety of mechanisms. Metapopulation dynamics can be disrupted, as settlement and/or dispersal movements may be impeded by a hostile matrix (Opdam 1991, Gobeil and Villard 2002). While neotropical migrant songbirds are highly vagile, predation risk during the breeding season reduces their willingness to be exposed (Harris and Reed 2002). Gap-crossing behaviour can be influenced by gap width (Desrochers and Hannon 1997), proximity of the closest forest cover (Bélisle and Desrochers 2002), degree of forest dependence of the species (St.-Clair 2003), and the sex of the individual (Norris and Stutchbury 2002). Pairing success has been identified as a factor affected by isolation (Willson 2004, Lampila et al. 2005). Isolation does not affect habitat quality within, rather movement between, fragments, and while patch occupancy can reveal patterns linked to dispersal (Hanski 1998), thorough analysis requires studies focused on demography .

A decrease in habitat quality due to a change in the quality or quantity of food resources, nest-sites, or in the availability of, or access to, mates (Bayne and Hobson 2002) affects breeding success. This, in turn, can influence female site fidelity, as females tend to avoid returning to areas where previous breeding attempts were unsuccessful (Muller et al. 1997, Cooper and Walters 2002, Hoover 2003). Younger, less

experienced males may be relegated to lower quality habitat, thereby reducing reproductive success in these areas (Holmes et al. 1996, Bayne and Hobson 2001, Zanette 2001). Abundance patterns alone are generally regarded as insufficient when assessing habitat quality (Van Horne 1983, Vickery et al. 1992). Fitness, a true measure of habitat quality, can be evaluated by monitoring pairing status and reproductive success (Donovan et al. 1995, Zanette 2001, Armstrong 2005).

Changes in vegetation structure for habitat specialists such as the black-throated green warbler may contribute to a population decline, yet to effectively determine the effects of vegetation change, preferred habitat attributes must be identified. To characterize habitat selection, it is necessary to understand its hierarchical nature. Johnson (1980) identifies four orders of habitat selection: first-order is the geographical range of a species, second-order is the home range of an individual or group, third-order refers to the use of the various habitat components within a territory, and fourth-order is micro-scale selection of areas for food attainment and selection of nest sites. Habitat use at multiple scales can differ, and if not appropriately identified, may have serious implications when integrating forest management with wildlife conservation (Young et al. 2005).

Artificial nest predation studies at Calling Lake indicate that local edge creation does not increase predation levels (Song and Hannon 1999, Cotterill and Hannon 1999), and very low numbers of brood parasites have been detected in the area (F. Schmiegelow, *unpubl. data*, M.-A. Villard and S. Hannon, *unpubl. data*). Parasitism and predation rates along edges in forested systems are generally low compared to the rates in agricultural systems, where the matrix is more permanent (Bayne and Hobson 1997, Ibarzabal and

Desrochers 2001, Chalfoun et al. 2002). However, area effects have not been directly examined, nor has habitat selection been identified in mapped territories. Previous research in this system (Song 1998) examined edge avoidance in 50-m intervals, between natural and anthropogenic edges. Fitness, measured by pairing status and reproductive success, has also not been evaluated for this species at Calling Lake. While isolation effects are associated with fragmentation (Hagan et al. 1996), they were not addressed in this study since the experimental design required that all fragments experienced the same level of isolation from continuous forest blocks.

The objectives of this chapter are to explore the processes underlying the pattern observed in Chapter 2, by:

1) Determining if *area effects* influenced mean abundance of black-throated green warblers, by comparing the observed trends in forest patches of varying sizes between control and fragment sites.

2) Determining if *edge effects* occurred by:
   a) testing if differential changes in vegetation attributes selected by black-throated green warblers occurred between fragments and controls.

   b) establishing if birds avoided site edges in fragments or in controls.

3) Determining if *habitat quality* differed between treatments by:
   a) comparing territory size between fragments and controls.

   b) testing for differences in fitness between fragment and control territories, expressed through pairing status and reproductive success.

3.2 METHODS

3.2.1 Study Area

This study was conducted in the 10, 40 and 100-ha fragment and control sites of the Calling Lake Fragmentation Experiment near Calling Lake, AB (55° 13' N, 113° 19' W). See Chapter 2 for further descriptions of the study area and experimental design.

3.2.2 Point counts

Point count surveys were conducted from 1993 through 2004 throughout the isolated forest fragment and continuous forest control sites (hereafter referred to as 'fragments' and 'controls', respectively). See Chapter 2 for a detailed explanation of the point count surveys. Average abundance of black-throated green warblers at point count stations was calculated to evaluate area effects. These surveys were also used as a systematic method of aurally searching all sites to detect black-throated green warbler individuals during territory establishment.

3.2.3 Population-level Surveys

Population-level surveys for black-throated green warblers were conducted during 2003 and 2004 to map territories, determine habitat use, and estimate fitness. A pair of observers spent up to fifteen minutes conducting a 100-m radius passive search until an individual was detected visually or aurally. These searches occurred where singing males had been detected during point counts or, for subsequent visits, within previously marked territories. If there was no detection during this initial passive search, conspecific playbacks were broadcast at a previously flagged location for 10 minutes to attract an individual. Playbacks consisted of a continuous recording of both A and B song types, which denote territoriality and mate attraction, respectively (Morse 1967, 1970), as well as call notes, compiled from the Birds of North America CD set (Brigham, no date). Playbacks were broadcast from a single-speaker tape player at a volume similar to that of actual bird song intensity (Harris and Reed 2001), and were restricted to locations of previous detections to minimize individuals being lured beyond their territory boundary.

Once a bird was detected, the tape was stopped, and one observer flagged used trees and recorded information regarding bird behaviour, tree species, and time of day, while the other observer maintained visual contact, noting when the bird changed behaviours or flew to another tree. All trees used by the bird were flagged, except the first one, as the response to the playback may have biased selection. Trees were marked where individuals exhibited singing, calling, foraging, preening, or carrying of food or nest-material behaviours. Males were followed for up to 30 minutes within a single hour-long visit, and up to 90 minutes across multiple visits during the breeding season (Lambert and Hannon 2000). Female detections were mapped opportunistically; however, as few females were detected, these locations were not included in analyses. If during a tracking bout a female was detected, or a male was observed carrying food, the territory was assigned a classification of 'paired'. No detections of polygamy were noted. Behaviours detected during tracking were used as a proximal index for fitness, and were used to assign reproductive ranks (Table 3.1), modified from Vickery et al. (1992). Tracking bouts occurred throughout the day, from 0500 hrs to 1600 hrs.

All tracking was conducted using observer pairs, as continuous tracking was necessary to ensure trees used for all behaviours, not just singing, were recorded. As black-throated green warblers sing from the canopy (T. Hannah, *pers. obs.*), they can be difficult to detect visually. Multiple observers and continuous tracking ensured the accuracy of the behavioural observations and spatial locations. Patterns of flight were highly variable, with both short (i.e. between adjacent trees) as well as long (>200-m across the territory) flights documented. While statistical autocorrelation occurs when using the continuous tracking method, it often leads to under- rather than over-estimation

of territory size (Swihart and Slade 1985, Barg et. al 2005). The addition of behaviours not regularly observed was considered of greater importance than reducing autocorrelation (De Solla et al. 1999).

Table 3.1 Reproductive ranks with associated observed behaviours.

Rank	Definition	Behaviours
1	Territorial† male present	Singing Calling Foraging Preening Territorial Dispute
2	Territorial pair present	Pair detected
3	Nest building	Carrying nesting material Distraction Display
4	Incubating or feeding hatchlings	Nest located Carrying Food
5	Confirmation of fledging success	Fledgling observed

† Territory defined as a minimum of 25 locations across 3 visits each ≥10 days apart

As individuals were not colour banded, and thus were not uniquely identifiable, spatial overlap of points and reuse of specific trees over the season suggested territoriality, and in some instances unique song patterns confirmed the identity of a particular male. At the end of the breeding season, flagged trees were spatially referenced using Trimble® GPS units. More individuals were detected and tracked than the final number of territories registered (see section 3.2.5), thus the numbers of territories presented here do not suggest actual density of individuals.

3.2.4 Vegetation Sampling

To evaluate vegetation change over time, I used plots established at a subset of point count stations within the study area, stratified by treatment and stand type. These plots were sampled in 1993 or 1994, and re-sampled in 2003. Four 0.04-ha plots were sampled at each station (see Schmiegelow et al. 1997), with one centered at the point count station, and the remaining 3 at 40-m distances at 0, 120, and 240 degrees. All trees within each plot were identified to species, categorized into four diameter at breast height (dbh) size classes: 8.0-15.0 cm, 15.1-23.0 cm, 23.1-38.0 cm, and >38.0 cm, and enumerated. All snags ≥8.0 cm were also tallied within the plot, but were not separated into dbh categories. This attribute was included as an indirect measure of tree damage or death. Only vegetation attributes selected by black-throated green warblers (see below) were evaluated for change over time.

Habitat selection by black-throated green warblers was assessed at two scales: within the territory (Johnson's 3rd order of habitat selection) and at the stand-level (Johnson's 2nd order of habitat selection; Johnson 1980). To examine within-territory selection, a random subset of used trees from the territory mapping was surveyed in 2004. Both dbh and species were recorded on used trees, as well as on all other trees ≥8 cm dbh that were unused (i.e. not flagged; hereafter termed 'available') within an 11.3-m radius circle (=0.04-ha) surrounding the used tree (Figure 3.1). If two randomly selected used trees were found to be within 11.3-m of each other, one was omitted and an alternate used tree was selected from within the same territory. All nest trees (n=28) had the same attributes recorded and were included as used trees in the analyses. At the stand level, all used and available trees measured within the territory were combined and referred to as

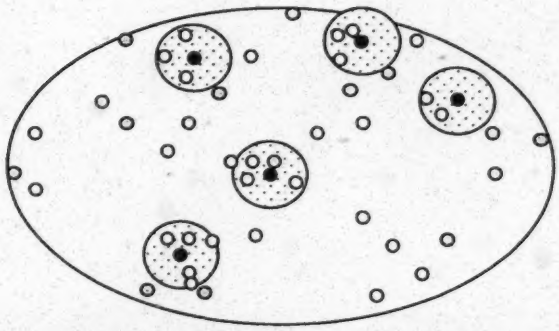

Figure 3.1 Schematic of vegetation sampling within a black-throated green warbler territory. Small, open circles are available trees, light grey are flagged trees (used), of which ~5 per territory were randomly selected (black circles). All available trees ≥8-cm within an 11.3-m radius circle (hatched) surrounding the used trees had species and dbh recorded.

'used' when compared to 'available' extra-territorial vegetation attributes gathered from an equal number of randomly selected point count vegetation plots, located throughout the study area and sampled in 2003. Species and dbh of all trees ≥8.0-cm dbh from the point count plots ('available') were compared to within-territory ('used') trees.

3.2.5 Territory Delineation

Spatially-referenced data points obtained using GPS units were uploaded into GPS Pathfinder Office 3.0 (Trimble Navigation Limited) and corrected using base station files provided by Alberta-Pacific Forest Industries, resulting in an error of <1m. The corrected points were imported into ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA) for analyses. Number of locations per territory was plotted against territory area to determine the asymptote defining the minimum number of points needed for territory delineation (Lambert and Hannon 2000). A cutoff of 25 locations, which resulted in 80% of the territory size estimate, was selected in order to maintain a sufficient sample size for analyses. Territories were thus delineated where a minimum of

25 locations, across 3 visits each separated by 10 days, existed. Territory boundaries were generated using 'floating amean' 95% minimum convex polygons (MCP), an iterative process where the mean of all points is calculated, then the farthest point is dropped and a new mean is calculated, continuing until only 95% of the points remain (Rodgers and Carr 1998). Dropping the outermost 5% of the points excluded those most likely to be erroneous due to misidentification of individuals where territories abutted or overlapped. While kernel density estimates (Worton 1989) generated more accurate contours around the data points, they also exceeded the territory boundaries created by connecting the points. As many black-throated green warblers seemed to establish their territory boundaries at stand edges (T. Hannah, *unpubl. data*), MCP methods ensured unused stands were not included in analyses. While these territory delineations do include areas that may be 'unused' within the territory boundaries, in order to compare with other studies, and to avoid other problems identified with kernels estimates (see Hemson et al. 2005), the MCP method was considered most appropriate. The largest source of spatial error was due to the digital vegetation map (Alberta Vegetation Inventory (Nesby 1997), hereafter AVI), which carries a 20m error, introduced by the interpolation from 1:20 000 aerial photographs. AVI derivation of stand origin is from a combination of overstory height and tree coring, and species composition is assigned to each stand in increments of 10% (Alberta Environmental Protection 1994). The digital AVI for the study area was updated in 2001/2002, and projected in NAD27 Zone 12.

3.2.6 Spatial Analyses

Comparison of stand-level attributes of occupied vs. random territories consisted of two approaches. Each approach included a matched 1:1 comparison between occupied

and random territories, but the definition of 'available' was altered to examine two scales of selection. 'Random Landscape' compared occupied territories to random territories within all sites in the study area. 'Random Site' compared occupied territories to random territories located within the originating site. For the first approach (Random Landscape), an equal number of random points as the number of territories was generated; each was given a unique ID, and placed anywhere within the study area. Next, each territory was assigned a random ID number, and then the polygon was copied, randomly rotated, and centered on the random point of matching ID. If the random placement overlapped a site boundary, the territory was shifted so that it was fully within the plot and still encompassed the random point, however may not be still centered on the point. The second approach was similar, except instead of generating random points anywhere in the study area, an equal number of random points were generated within each site as the documented number of territories. This resulted in each occupied territory having a matched, random territory within the same site. The same adjustment was made with territories overlapping site boundaries as with the previous approach.

Territory boundaries were used to clip the underlying AVI digital map for determination of stand-level territory composition. Area-weighted stand metrics describing stand age, height, and composition for each territory were derived using ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA) with the Xtools extension (DeLaune 2003). MCPs were used to compare territory size (area) between fragments and controls, and to determine minimum distance of MCP boundary to nearest site edge for edge avoidance analysis. An additional analysis was conducted comparing edge avoidance between used GPS locations associated with territories and an equal

number of randomly generated points for fragments and controls, respectively. Random points were generated within the study sites using Hawth's tools (Beyer 2005) for ArcGIS 8.2 (Environmental Systems Research Institute, Redlands, CA). For both edge avoidance analyses, the site edge refers to the forest-clearcut boundary in the fragments, and the boundary of the surveyed area in the controls.

3.2.7 Statistical Analyses

All tests were performed using SPSS 13.0 (2004), except case-controlled logistic regression which was conducted using Intercooled STATA 9.0 (2005). Non-parametric tests were used if the data could not be transformed to meet assumptions of normality (Zar 1999). Means are presented ± one standard deviation. Differences were considered significant at $\alpha = 0.10$, to minimize Type II errors, which are of concern in conservation-related research (Smith 1995).

3.2.7.1 Area effects

Numbers of black-throated green warblers at each point count station were summed across visits within a breeding season, and divided by the number of visits to yield an average abundance per station per year. The effect of patch size was examined using a repeated measures analysis of variance to test for main (treatment, size) and interaction effects on average abundance over time (1993-2004). The data were averaged within a 'treatment x patch size' category for each year to generate separate population trends, then analyzed using linear regressions to compare coefficients of the interactions, followed by t-tests to evaluate differences between the slopes. A Bonferroni adjustment for multiple comparisons established the critical alpha-level for these tests.

3.2.7.2 Edge Effects

Vegetation Selection and Vegetation Change

Four tree species were dominant in vegetation plots, with other species rarely appearing. Thus, only trembling aspen, white spruce, paper birch and balsam poplar were included in analyses. Chi-square tests were used to compare use vs. availability of tree species within territories, as well as use vs. availability of tree species for different bird behaviours, following Neu's selection ratio (Neu et al. 1974, McClean et al. 1998, Manly et al. 2003). T-tests evaluated differences in average diameter at breast height (dbh) between used and available trees, for each tree species. Average dbh between used and available trees within each tree species, and associated with each behaviour, was evaluated using Mann-Whitney U tests. For this analysis, trees that were used more than once, for different behaviours, were included multiple times.

At the stand-level, use vs. availability was examined for tree species of different dbh size classes using chi-square tests. Case-controlled logistic regression was used to contrast territory composition of occupied vs. random territories; this analysis was performed twice, corresponding to different scales of selection (see Section 3.2.6).

Vegetation change from 1993/94 to 2003 was evaluated using a Wilcoxon-signed ranks test. Chi-squared tests were used to examine notable patterns of change for certain vegetation attributes.

Edge Avoidance

Average minimum distance of territory boundary to nearest site edge between treatments was evaluated using a Mann-Whitney U test. An analysis of variance was

conducted to compare the effects of treatment, location type (occupied or random), and the interaction of these two effects to test whether distance of point locations to site edge differed between fragments and controls.

3.2.7.3 Habitat Quality

Territory size estimates derived from 95% MCPs were compared between fragments and controls using a Mann-Whitney test. Differences in pairing status and reproductive success between fragment and control territories were examined using a Chi-square and a Wilcoxon-signed ranks test, respectively.

3.3 RESULTS

Abundance estimates in 2003 and 2004 derived from point count surveys, tracked birds, and territory delineation indicate some discrepancies in both absolute and relative abundance estimates between the various techniques (Table 3.2). More individuals were identified through tracking than point counts, particularly in the fragments, whereas many fewer individuals were determined to be territorial. Note the estimates derived from territory delineation were dependent on the definition of a territory applied in this study, i.e. a minimum of 25 locations across 3 visits, each 10 days apart. A relaxation of these criteria would have increased the abundance estimates derived from territory delineation methods, to levels more similar to those derived from the point count and tracking methods.

3.3.1 Area Effects

There was no significant effect of treatment or size on average abundance over the 12 years (repeated measures analysis of variance, treatment F=0.59, p=0.44, size

Table 3.2 Comparisons of black-throated green warbler abundance estimates in 2003 and 2004 using three methods.

Year	Method	Abundance estimate	
		Controls	Fragments
2003	Point Count	21.0	12.3
	Tracking	23	19
	Territory Delineation	12	5
2004	Point Count	15.3	11.0
	Tracking	17	15
	Territory Delineation	14	8

F=1.60, p=0.20), but a significant interaction was detected (treatment x size F=3.09, p=0.048). Each treatment x size combination (n = 6) was evaluated using linear regression, and the slopes were compared to establish if the interaction effect was occurring in the smaller fragments, as predicted by fragmentation theory. All categories demonstrated a negative coefficient, thus exhibiting a decline over the 12 years (Figure 3.2), with 5 of the 6 categories showing a significant decline (Table 3.3). Slopes ranged from -0.010 (10-ha controls) to -0.054 (40-ha fragments). Line fit ranged from poor (R^2 = 0.115, 10-ha controls) to strong (R^2 = 0.80, 40-ha fragments). T-tests comparing coefficients identified 10-ha fragments and 40-ha fragments as having significantly different slopes from each other, and from 40- and 100-ha controls, and 10-ha controls and 100-ha fragments, respectively (Table 3.4). Categories were grouped as follows, with sites sharing similar slopes underlined:

F-10 C-10 F-100 C-40 C-100 F-40

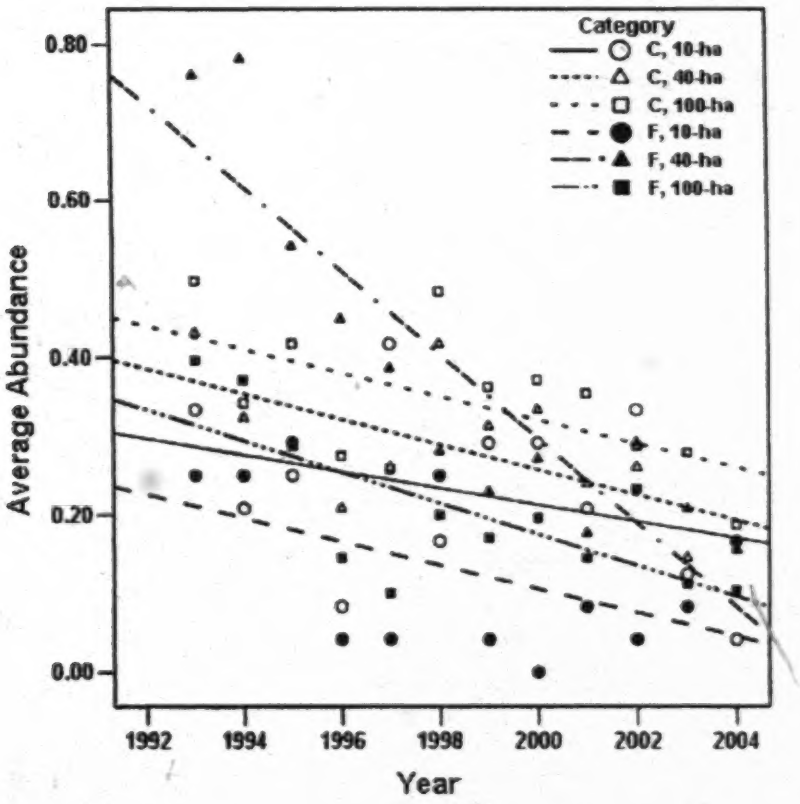

Figure 3.2 Linear regressions depicting average abundance per point count station of black-throated green warblers for each size x treatment category. First data point (1993) is pre-harvest, followed by 11 years of post-harvest data. C=controls, F=fragments.

Table 3.3 Results from linear regressions for size x treatment categories. Independent variable is year (1993-2004); dependent variable is average abundance at a point count station. C=Controls, F=Fragments.

Category	Intercept	β	SE	*t*	R^2	*p*-value
C, 10-ha	21.19	-0.010	0.009	-1.14	0.115	0.282
C, 40-ha	32.14	-0.016	0.006	-2.65	0.413	**0.024**
C, 100-ha	30.12	-0.015	0.007	-2.27	0.340	**0.047**
F, 10-ha	30.14	-0.015	0.008	-1.88	0.262	**0.089**
F, 40-ha	107.31	-0.054	0.008	-6.40	0.804	**0.000**
F, 100-ha	39.72	-0.020	0.006	-3.23	0.510	**0.009**

* bold denotes significance at $\alpha = 0.10$

Table 3.4 Comparisons of coefficients from linear regressions for size x treatment categories. Independent variable is year (1993-2004); dependent variable is average abundance of black-throated green warblers at a point count station. Results displayed are the p-value followed by the t-statistic in parentheses. C= Controls, F=Fragments; bold denotes significance at a Bonferroni-adjusted alpha of 0.007.

Category	C 10-ha	C 40-ha	C 100-ha	F 10-ha	F 40-ha	F 100-ha
C, 10-ha						
C, 40-ha	0.32 (1.00)					
C, 100-ha	0.03 (-2.18)	0.25 (1.17)				
F, 10-ha	0.05 (-1.96)	**0.004** (-2.97)	**<0.001** (-4.16)			
F, 40-ha	**0.006** (2.85)	0.07 (1.84)	0.52 (0.65)	**<0.001** (4.79)		
F, 100-ha	0.63 (-0.48)	0.14 (-1.49)	0.01 (-2.68)	0.15 (1.47)	**0.001** (-3.35)	

3.3.2 Edge Effects

3.3.2.1 Vegetation Selection and Vegetation Change

i. Vegetation Selection: Territory-level

A total of 256 trees used by 56 male black-throated green warblers in 2003 & 2004 were sampled (n =157 in controls, n =99 in fragments), as were 4534 available trees (n =2916 in controls, n =1617 in fragments) from associated 11.3-m radius vegetation plots.

White spruce use by black-throated green warblers (all behaviours combined) was significantly more than expected, in fragments, controls, and in both treatments combined (Table 3.5). Trembling aspen was used less than expected in fragments and in both treatments combined. No other selection for tree species was detected. All subsequent analyses examining use vs. availability combine controls and fragments. For both

foraging and singing, white spruce was used significantly more than expected, while paper birch was used less than expected (Table 3.6). However, paper birch was used significantly more than expected for nesting, while trembling aspen was used less than expected. For each of the 4 tree species, dbh of used trees was significantly greater than available trees (Table 3.7). Difference in dbh between used and available trees depended on the tree species, and ranged from 4.6 cm (paper birch) to 20.9 cm (white spruce).

Comparing average dbh between used and available trees within each tree species, for each behaviour, indicated that for singing, used trees had a larger average dbh compared to available trees for all tree species (Table 3.8). For foraging, all tree species except paper birch had a larger average dbh for used trees compared to available trees (all $p < 0.012$). A total of 28 nests were located in 2003 and 2004. Paper birch (65%) and white spruce (21%) trees used for nesting had a larger average dbh than available trees of each species (paper birch, $U=4010.5$, $p=0.005$; white spruce, $U=992.0$, $p=0.029$). There was no difference in dbh of balsam poplar nesting trees (14%) compared to available balsam poplar trees ($U=1642.0$, $p=0.290$); no nests were found in trembling aspen.

ii. Vegetation Selection: Stand-level

Trees (used + available, $n= 4789$) from 256 territory plots were compared to available trees ($n=5487$) from 256 random vegetation plots by species and dbh to evaluate stand compositions (Table 3.9). In general, black-throated green warbler territories contained more large trees than expected for all 4 tree species. Trees of dbh >38.0 cm were used significantly more than expected for trembling aspen, balsam poplar, and white spruce; less than 5 paper birch trees >38.0 cm dbh were measured, thus this category was not included in the analyses. White spruce with a dbh of 23.1 – 38.0 cm

(Class 3) was also used more than expected. Larger paper birch (in dbh Classes 2 and 3) were used more than expected, whereas paper birch of Class 1 (8.0-15.1 cm) were used less than expected.

Case-controlled logistic regression comparing occupied to random territory composition used area-weighted stand age, stand height and percent white spruce calculated for 39 occupied territories and 39 random territories. Stand age and stand height were correlated based on Pearson's correlations ($r > |0.8|$) thus stand height was dropped from further analyses, as stand age was determined to be of greater use for forest management planning (G. Dribnenki, *pers. comm.*). Average stand age for occupied territories was 120.5 years, and average percent white spruce was 12% (Table 3.10). Both area-weighted stand age (age) and area-weighted white spruce (sw) were significant predictors of occupied territories across the study area (age, p=0.03; sw, p=0.07). Comparisons constrained to the originating site (i.e. occupied vs. random site) yielded significance only in area-weighted stand age (age, p=0.03; sw, p=0.55).

iii. Vegetation Change: Selected Attributes

A total of 240 vegetation plots throughout the study area were sampled in both 1993/94 and 2003. Six variables selected by black-throated green warblers (listed in Table 3.11), along with snag abundance, were evaluated for change. The only significant increases occurred in abundance of 23.1-38.0 cm dbh white spruce in controls, and in snag abundance in fragments. A significant decrease was exhibited by paper birch in both treatments for size classes 15.1-23.0 cm and 23.1-38.0 cm (all p<0.03). Balsam poplar larger than 38.0 cm dbh decreased in both controls (p=0.014) and fragments (p=0.013); trembling aspen larger than 38.0 cm dbh decreased in the fragments (p=0.084)

but not in the controls (p=0.350). Of the 7 variables tested over time, 3 trends differed between the controls and fragments: white spruce 23.1-38.0 cm dbh (up in F, no change in C); trembling aspen >38.0 cm dbh (no change in C, down in F) and snag abundance (no change in C, up in F); see Table 3.11.

As paper birch demonstrated a significant decline throughout the study area, this pattern was examined in more detail. Density and basal area estimates of paper birch decreased from 1993/94 to 2003, and were overall lower within the study area compared to estimates from within territories (Table 3.12). Based on the stem density decrease, the estimated mortality over the 10-year period is 33%. Chi-square values indicate paper birch distributions differed significantly from a normal distribution, thus exhibiting a clumped distribution, for point count plots in both years and for territory plots (Table 3.12 and Figure 3.3).

3.3.2.2 Edge Avoidance

Minimum distance to nearest site boundary for the 95% MCP polygons was determined for all territories, with control territories (n=26) averaging 47.23 ± 71.20 m to edge, and fragment territories (n=13) averaging 70.82 ± 60.91 m to edge. Differences in distance to edge between control and fragment territories was significant (Mann-Whitney, U=102.0, p=0.043; Table 3.13).

The difference in mean distance to edge between used control points (n=954) and used fragment points (n=463) is 31.75-m (Table 3.13). The analysis of variance comparing distance to edge showed a significant difference in the treatment effect (F=32.37, p<0.001), but not in the location type (used or random, F=0.922, p=0.34). The interaction between treatment and location type (used or random) was significant

(F=19.62, p<0.001). Used points in fragments were significantly further from the edge than random points or used control points.

3.3.3 Habitat Quality

A total of 39 territories, each with a minimum of 25 locations, across 3 visits each separated by 10 days, were mapped and monitored during the 2003 and 2004 breeding seasons: 26 in the control sites and 13 in the fragment sites (see Figure 3.4 for examples of territory delineations). Dates of tracking ranged from May 13 through July 2 in 2003 and May 19 through July 7 in 2004; further tracking statistics are summarized in Table 3.14. Territory size (area of 95% MCP) in controls (n=26, 0.54 – 4.54 ha, $\bar{x}$ = 2.03 ± 1.19) and fragments (n=13, 0.20 – 6.12, $\bar{x}$ = 2.58 ± 1.83) did not differ (U=145.0, p=0.48). Sixty-nine percent of control (18/26) and 92% of fragment territories (12/13) had females, however differences in pairing status were not statistically significant (χ^2= 2.6, df=1, p=0.107). There was no significant difference in distribution of reproductive ranks between control and fragment territories (Z = -1.604, p=0.109; Figure 3.5). However, the marginal nature of the p-values (near significance at α=0.10), in conjunction with relatively low power due to small sample sizes warrants further consideration.

3.4 Discussion

I explored the processes underlying the pattern of decline in black-throated green warblers in experimentally created forest fragments by evaluating area and edge effects, and measures of habitat quality.

Table 3.5 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use for tree species within black-throated green warbler territories based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected use (+; bold), significantly less than expected use (-; bold) or no difference (0), at $\alpha = 0.10$.

Species	Expected Use	Observed Use	90% Bonferroni CI		Selection
			Lower	Upper	
Controls & Fragments:					
Trembling aspen	0.429	**0.328**	0.271	0.385	-
Paper birch	0.159	0.143	0.100	0.185	0
Balsam poplar	0.261	0.259	0.205	0.312	0
White spruce	0.151	**0.270**	0.216	0.324	+
Fragments:					
Trembling aspen	0.417	**0.255**	0.170	0.339	-
Paper birch	0.112	0.147	0.078	0.216	0
Balsam poplar	0.387	0.363	0.269	0.456	0
White spruce	0.085	**0.235**	0.153	0.318	+
Controls:					
Trembling aspen	0.436	0.376	0.300	0.452	0
Paper birch	0.185	0.140	0.086	0.194	0
Balsam poplar	0.191	0.191	0.130	0.253	0
White spruce	0.188	**0.293**	0.222	0.364	+

Table 3.6 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use for behaviours associated with tree species within black-throated green warbler territories based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected use (+; bold), significantly less than expected use (-; bold) or no difference (0), at $\alpha = 0.10$.

Species	Expected Use	Observed Use	90% Bonferroni CI		Selection
			Lower	Upper	
Singing:					
Trembling aspen	0.429	0.406	0.338	0.474	0
Paper birch	0.159	**0.059**	0.027	0.092	-
Balsam poplar	0.261	0.277	0.215	0.339	0
White spruce	0.151	**0.257**	0.197	0.318	+
Foraging:					
Trembling aspen	0.429	0.392	0.285	0.500	0
Paper birch	0.159	**0.089**	0.026	0.151	-
Balsam poplar	0.261	0.253	0.157	0.349	0
White spruce	0.151	**0.266**	0.168	0.363	+
Nesting:					
Trembling aspen	0.429	**0.000**	0.000	0.000	-
Paper birch	0.159	**0.643**	0.465	0.820	+
Balsam poplar	0.261	0.143	0.013	0.272	0
White spruce	0.151	0.214	0.062	0.366	0

Table 3.7 Average diameter at breast height (dbh) for used trees (all behaviours combined, n=256) vs. available (n=4534) trees of 4 tree species within black-throated green warbler territories.

Species	Used dbh $\bar{x}$ (min-max) (cm)	Available dbh $\bar{x}$ (min-max) (cm)	t	p-value*
Trembling aspen	39.2 (12.9-72.0)	27.6 (8.0-67.3)	7.92	**<0.001**
Paper birch	21.2 (7.3-35.6)	16.6 (7.5-51.6)	4.94	**<0.001**
Balsam poplar	42.6 (11.6-83.4)	31.5 (8.0-71.8)	6.25	**<0.001**
White spruce	47.8 (3.8-77.8)	26.9 (8.0-74.8)	11.45	**<0.001**

* bold denotes significance at $\alpha = 0.10$

Table 3.8 Results of Mann-Whitney U analyses comparing average dbh between used and available trees within black-throated green warbler territories. Comparisons are made within tree species and behaviour. Tests are two-tailed; bold denotes significance at $\alpha = 0.10$.

Species	Used or Available	*n*	$\bar{x}$ dbh (cm)	Mann-Whitney U	*p*-value
Singing:					
Trembling Aspen	Used	82	39.5	40886.0	**<0.001**
	Available	1945	27.6		
Paper Birch	Used	12	22.1	2474.5	**0.011**
	Available	722	16.6		
Balsam Poplar	Used	56	42.9	18870.0	**<0.001**
	Available	1183	31.5		
White Spruce	Used	52	50.2	4905.5	**<0.001**
	Available	684	26.9		
Foraging:					
Trembling Aspen	Used	31	35.1	19883.5	**0.001**
	Available	1945	27.6		
Paper Birch	Used	7	21.1	1891.5	0.252
	Available	722	16.6		
Balsam Poplar	Used	20	37.7	8690.5	**0.042**
	Available	1183	31.5		
White Spruce	Used	21	45.9	2787.5	**<0.001**
	Available	684	26.9		
Nesting:					
Trembling Aspen	Used	0	n/a	n/a	n/a
	Available	1945	27.6		
Paper Birch	Used	18	21.4	4010.5	**0.005**
	Available	722	16.6		
Balsam Poplar	Used	4	38.0	1642.0	0.290
	Available	1183	31.5		
White Spruce	Used	6	42.1	992.0	**0.029**
	Available	684	26.9		

Table 3.9 Results of chi-squared analyses based on Neu's selection ratio comparing observed vs. expected use by black-throated green warblers of dbh size classes of different tree species. Comparisons are between territories and available stands, based on 90% Bonferroni confidence intervals. 'Selection' indicates observed use was significantly greater than expected (+; bold), significantly less than expected (-; bold) or no difference (0), at $\alpha = 0.10$.

Species	Expected Use	Observed Use	90% Bonferroni CI		Selection
			Lower	Upper	
Trembling Aspen:					
Class 1 (8-15 cm)	0.208	0.189	0.172	0.206	0
Class 2 (15.1-23 cm)	0.391	**0.260**	0.241	0.279	-
Class 3 (23.1-38 cm)	0.334	**0.278**	0.258	0.297	-
Class 4 (>38 cm)	0.067	**0.273**	0.254	0.292	+
White Spruce:					
Class 1 (8-15 cm)	0.487	**0.317**	0.284	0.351	-
Class 2 (15.1-23 cm)	0.299	**0.127**	0.104	0.151	-
Class 3 (23.1-38 cm)	0.141	**0.228**	0.198	0.258	+
Class 4 (>38 cm)	0.073	**0.327**	0.293	0.360	+
Balsam Poplar:					
Class 1 (8-15 cm)	0.300	**0.160**	0.140	0.180	-
Class 2 (15.1-23 cm)	0.225	**0.159**	0.139	0.179	-
Class 3 (23.1-38 cm)	0.269	0.290	0.265	0.316	0
Class 4 (>38 cm)	0.206	**0.390**	0.363	0.417	+
Paper Birch:					
Class 1 (8-15 cm)	0.708	**0.457**	0.424	0.490	-
Class 2 (15.1-23 cm)	0.215	**0.369**	0.337	0.401	+
Class 3 (23.1-38 cm)	0.077	**0.174**	0.149	0.199	+

Table 3.10 Summary statistics and results from case-controlled logistic regression comparing occupied black-throated green warbler territories to random territories within all sites in the study area (Random Landscape), and to territories randomly placed within the originating site (Random Site).

Territory type	$\bar{x}$ value†	β	SE	z	*p*-value*	90% C.I.	
						Lower	Upper
Occupied							
Stand Age (years)	120.5 ± 7.5	-	-	-	-	-	-
White Spruce (%)	0.12 ± 0.09	-	-	-	-	-	-
Random Landscape							
Stand Age (years)	107.6 ± 18.0	0.06	0.03	2.23	**0.03**	0.015	0.10
White Spruce (%)	0.06 ± 0.07	7.12	3.94	1.81	**0.07**	0.65	13.60
Random Site							
Stand Age (years)	111.6 ± 15.8	0.07	0.03	2.12	**0.03**	0.016	0.13
White Spruce (%)	0.09 ± 0.10	1.60	2.68	0.60	0.55	-2.81	6.00

† area-weighted metrics, derived from Alberta Vegetation Inventory stand attributes

* bold denotes significance at $\alpha = 0.10$

Table 3.11 Results from Wilcoxon-Signed ranks test evaluating vegetation change from 1993/94 to 2003 for vegetation attributes selected by black-throated green warblers. Direction over time refers to a significant increase (↑) or decrease (↓), or no change (0) in abundance levels of the vegetation attribute.

Species dbh class	Treatment	$\bar{x}$ 1993 2003	SD (min-max) 1993 2003	Direction over time	Wilcoxon Signed Ranks Test	
					Z	p-value*
Paper Birch 15.1-23.0 cm	C	0.70 0.52	1.38 (0-8) 1.21 (0-9)	↓	-2.352	**0.019**
	F	0.53 0.38	1.09 (0-6) 0.83 (0-5)	↓	-2.079	**0.038**
Paper Birch 23.1-38.0 cm	C	0.29 0.13	0.64 (0-3) 0.44 (0-3)	↓	-2.996	**0.003**
	F	0.29 0.19	0.66 (0-3) 0.73 (0-7)	↓	-2.441	**0.015**
White Spruce 23.1-38.0 cm	C	0.51 0.78	1.27 (0-7) 1.54 (0-8)	↑	-2.639	**0.008**
	F	0.21 0.25	0.86 (0-8) 0.84 (0-6)	0	-0.467	0.640
White Spruce >38.0 cm	C	0.38 0.32	0.92 (0-5) 0.79 (0-4)	0	-0.816	0.415
	F	0.18 0.19	0.69 (0-6) 0.51 (0-2)	0	-1.000	0.317
Balsam Poplar >38.0 cm	C	0.51 0.34	1.16 (0-6) 1.05 (0-5)	↓	-2.470	**0.014**
	F	1.15 0.75	2.09 (0-11) 1.26 (0-6)	↓	-2.485	**0.013**
Trembling Aspen >38.0 cm	C	1.06 0.88	1.94 (0-12) 1.56 (0-7)	0	-0.935	0.350
	F	1.20 0.89	1.77 (0-9) 1.40 (0-7)	↓	-1.727	**0.084**
Snags	C	5.00 5.30	3.62 (0-15) 3.37 (0-20)	0	-1.012	0.312
	F	3.33 3.93	3.01 (0-13) 3.22 (0-19)	↑	-2.507	**0.012**

* bold denotes significance at $\alpha = 0.10$.

Table 3.12 Estimated mean density and basal area of paper birch (15.0-38.0 cm dbh) at point count vegetation plots located throughout the study area, sampled in 1993/94 and 2003, and within black-throated green warbler territory plots sampled in 2004. Chi-square values evaluate distribution of stems across vegetation plots compared to a normal distribution.

Plot and Year	Dbh Class	Density (stems/ha)	Basal Area (m2/ha)	χ^2 (df)	p-value*
Point count 1993/94	15.1 – 23.0 cm	15.5	0.44		
	23.1 – 38.0 cm	7.2	0.53		
	TOTAL	**22.7**	**1.26**	**612.93 (7)**	**<0.001**
Point count 2003	15.1 – 23.0 cm	11.3	0.32		
	23.1 – 38.0 cm	4.0	0.29		
	TOTAL	**15.2**	**0.84**	**842.73 (7)**	**<0.001**
Territory 2004	15.1 – 23.0 cm	26.9	0.77		
	23.1 – 38.0 cm	12.8	0.94		
	TOTAL	**39.6**	**2.20**	**409.08 (9)**	**<0.001**

* bold denotes significance at $\alpha = 0.10$.

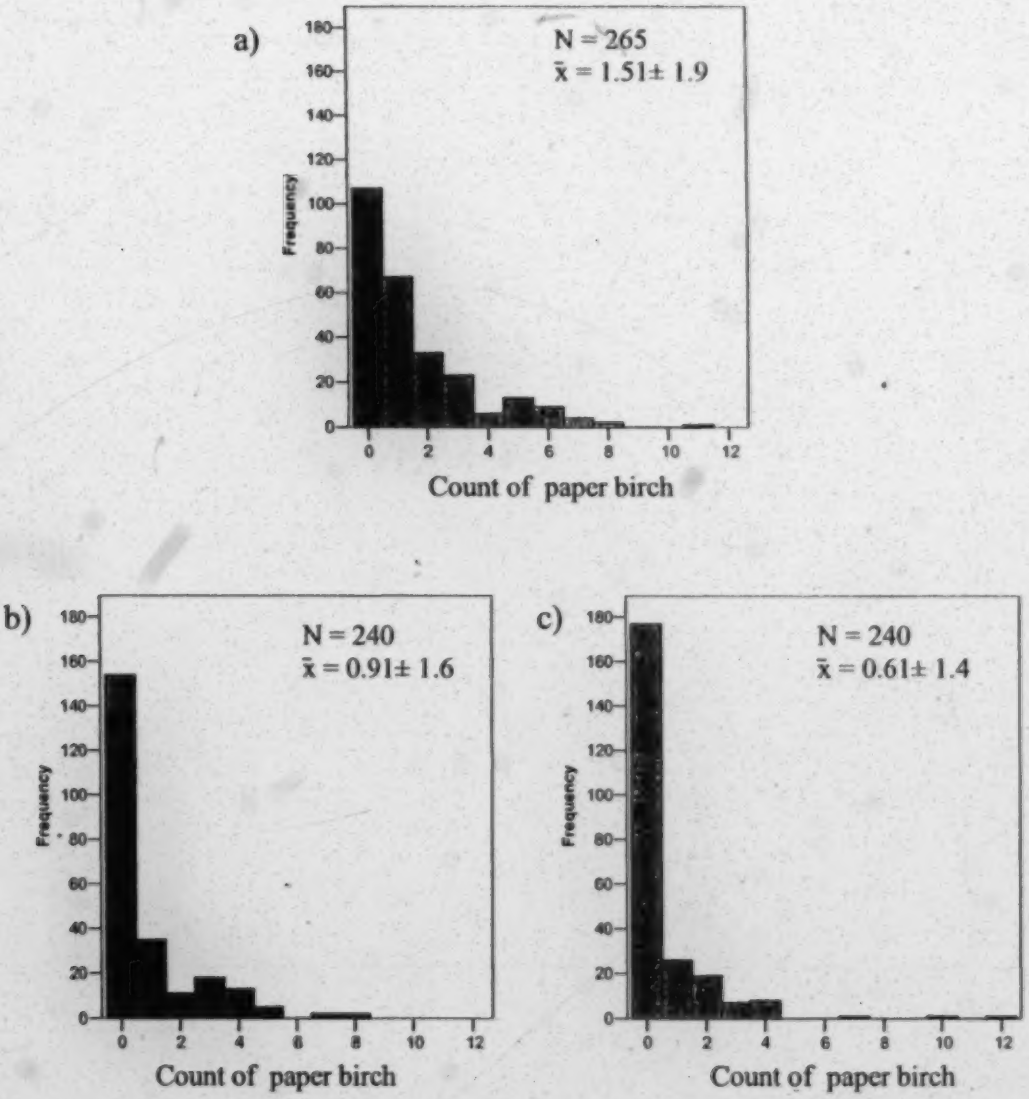

Figure 3.3 Frequency histograms of the number of vegetation plots with occurrence of paper birch stems; a) within black-throated green warbler territory plots sampled in 2003/2004; b) within point count plots located throughout the study area sampled in 1993 c) within point count plots located throughout the study area sampled in 2003.

Table 3.13 Summary of edge avoidance results comparing average distance of black-throated green warbler territory boundaries to nearest site edge between fragments and controls (MCP), and of average distance of point locations to nearest site edge between used and random points, for fragments and controls (Points).

		n	Distance to edge $\bar{x} \pm SD$ (m)	Range (min-max) (m)
MCP				
Controls		26	47.2 ± 71.2	0.0 – 293.8
Fragments		13	70.8 ± 60.9	3.7 – 248.0
Points				
Controls	Used	954	120.6 ± 78.4	0.6 – 392.4
	Random	954	132.6 ± 100.0	0.3 – 410.7
Fragments	Used	463	152.3 ± 78.1	0.6 – 392.4
	Random	463	136.1 ± 100.2	0.3 – 410.7

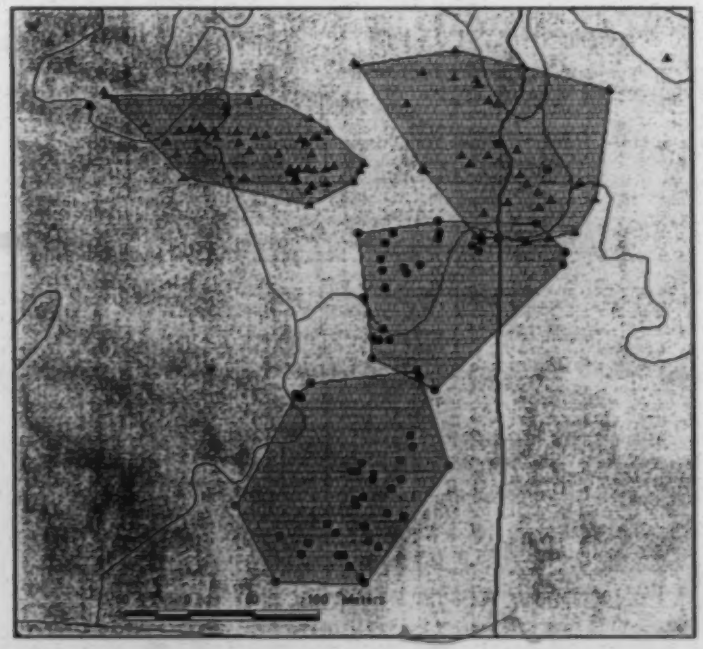

Figure 3.4 Four black-throated green territories in a 40-ha Control site. Territory boundaries for 2003 (triangles) and 2004 (circles) are delineated by 95% minimum convex polygons. The thicker black line bisecting image is the eastern site boundary; thinner black lines are Alberta Vegetation Inventory stand boundaries.

Table 3.14 Summary of tracking episodes for 2003 & 2004 combined, for each treatment. Territory is defined as a territorial male with a minimum of 25 locations across 3 visits each a minimum 10 days apart; n=39.

Attribute	Treatment	$\bar{x}$	SD	Range (min-max)
Number of Visits	Control	6.4	1.4	3-9
	Fragment	5.6	1.0	4-7
Number of Visits with Detections	Control	5.6	1.2	3-8
	Fragment	4.9	0.9	4-6
Number of Locations/Territory (GPS)	Control	41.5	15.0	26-76
	Fragment	35.6	10.0	26-55
Number of Locations/Visit†	Control	7.6	2.9	3.7-16.3
	Fragment	7.3	1.8	4.3-9.8
Total tracking interval (days)	Control	35.8	5.9	24-45
	Fragment	28.8	9.9	14-49

† Visit defined here as a "visit with a detection"

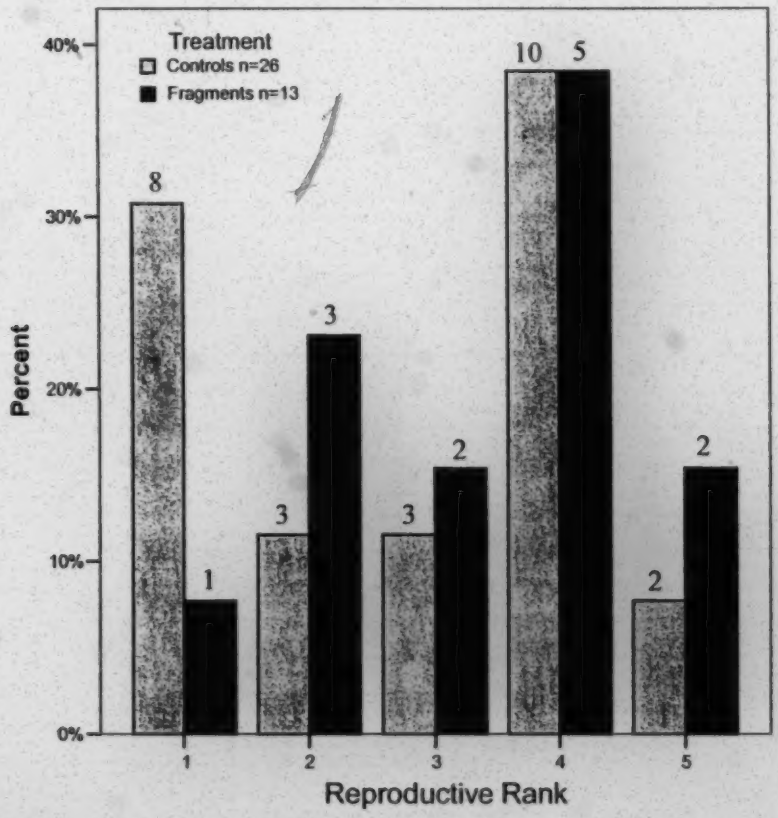

Figure 3.5 Proportion of black-throated green territories in each category of reproductive rank (see Table 3.1), for control and fragment sites. Values above bars indicate number of territories per rank.

3.4.1 Area effects

Significant differences between the slopes of the 10-ha and 40-ha fragment regression lines compared to most of the other treatment x size categories indicates a potential area effect. However, the 40-ha fragments, rather than the 10-ha fragments, exhibited the steepest slope. The larger intercept associated with the 40-ha fragments influenced the rate of the decline, as these sites supported the highest initial abundance of black-throated green warblers, thus had the greatest potential for decline. Nevertheless, apparent collapse of local populations in the 10-ha fragments by 1996, resulting in very low abundance levels subsequently, may have masked a linear patch size effect. While in principle, 10-ha is sufficient to accommodate several territories of this species (average territory size of 2.22-ha, see Section 3.3.3), given that black-throated green warblers are habitat specialists, the amount and arrangement of suitable habitat within the remnant patches influences the functional area of these sites. Edge effects may further reduce the functional area of the patch (Bollinger and Switzer 2002); however, as it is difficult to separate area effects from edge effects (Villard 1998, Parker et al. 2005), these results should be interpreted cautiously.

3.4.2 Edge Effects

3.4.2.1 Vegetation Selection and Change

Clear selection for trees with larger diameters was exhibited by black-throated green warblers. Larger white spruce were used more than all other species, and were preferred as songposts as well as for foraging, similar to findings by Robichaud and Villard (1999). The preference for large white spruce is most likely due to their canopy

emergence, allowing for song projection, and their foliage structure, which is ideally suited for tip gleaners (Robichaud and Villard 1999). Larger paper birch was avoided for singing and foraging behaviours, yet preferred for nesting. More than half of all nests were located in birch trees, in contrast to requirements documented in the eastern portions of the range, where nests are usually located in conifers (Morse 2005). The strong paper birch requirement for nesting, and the white spruce selection for foraging, as well as the larger dbh preference for both species, reinforces the importance of older mixedwood stands for this songbird, consistent with occupancy results from Chapter 2.

Selection of territory placement differed between scales, with analyses at the broader landscape scale suggesting a selection for white spruce that was not evident at a finer scale. This difference in selection can most likely be explained by the differing definitions of 'available' (McClean et al. 1998), which altered the range of variation in white spruce between the two scales. This demonstrates yet again the importance of identifying the appropriate scale when comparing use vs. availability, as different scales of analysis may produce different results (Young et al. 2005). Selection at a coarse-scale can mask finer-scale selection patterns (Johnson 1980, Thomas and Taylor 1990). As forest management planning occurs at a landscape-level, and as songbirds' habitat selection upon arriving on the breeding grounds is also at the landscape-level (Johnson's 2nd order), the landscape is an appropriate scale for interpreting the responses I observed. The preference for older forest (~120 years) with some white spruce (~12%) again substantiates the conclusions arrived at in Chapter 2, derived from coarse-scale surveys.

Black-throated green warblers selected larger trees of all species examined; large aspen, poplar and birch all decreased over time, likely due to natural forest succession

and death of canopy trees, or recent climate patterns; in particular, a series of relatively dry years with associated tree mortalities reported anecdotally throughout the region. This may have contributed to the decline in black-throated green warblers throughout the study area. However it has been shown by Smith and Dallman (1996) that black-throated green warblers in the eastern portion of their range use gaps more than expected, therefore should western individuals exhibit a similar behaviour, a decline in canopy trees may not have negative effects on this species, depending on the magnitude of the decline. Individuals also require larger white spruce in the overstory; this attribute either remained stable or increased over the time period studied. The only changes in selected vegetation attributes between fragments and controls that could possibly be attributed to edge effects were decreases in the number of large aspen, with associated increases in the abundance of snags in fragments. It seems unlikely that this has affected the fragment population of black-throated green warblers since large aspen were not selected for the behaviours I examined. Thus, it does not appear that differential vegetation change over time is responsible for the decline in the fragments. The vegetation plots were placed within 40-m of a point count station, thus the nearest they were to a site boundary (or edge in the fragments) was 65-m. There has been some debate over how far edge influences permeate a forest, however most boreal vegetation studies suggest between 25- and 100-m, depending on the response of interest (Harper et al. 2005). Depending on how far edge effects permeated the forest remnants in this study, the vegetation change noted here may be more indicative of natural change within the site interiors (e.g., Cumming et al. 2000) rather than compositional and structural change due to edge effects, *per se*, or some combination of the two. Vegetation changes may have contributed to the overall decline

in black-throated green warblers in the study area; however whether this change is a consequence of anthropogenic effects or natural forest succession, is unclear.

Paper birch was shown to be a rare and clustered resource, and occurred in higher densities and higher basal area within occupied territories compared to available sites. The decline of larger (15.1-38.0 cm) paper birch from 1993/94 to 2003 was consistent in both the control and fragments sites, and may be due to the relatively dry conditions experienced throughout Alberta over the last decade. The reduction in paper birch throughout the study area may have contributed to the overall population decline of the black-throated green warbler at Calling Lake. Large paper birch were selected for nesting, and the availability of nest trees may be a limiting resource for this songbird. However, nests were also found in two other tree species (white spruce and balsam poplar), suggesting that while the black-throated green warbler may prefer birch trees for nesting, they have some flexibility in this use.

Comparison with Other Regions

Townsend's warbler (*Dendroica townsendi*), the western representative of the *Dendroica virens* superspecies, breeds from n. Washington to s. Alaska. For this species in Alaska, optimal habitat occurred on steep slopes, which most likely aided in mate and territory defence, thermoregulation, and microclimate suitability for arthropod prey (Matsuoka et al. 1997). Gap use by black-throated green warblers in mature mixedwood forests in Michigan was also explained by potential increases in both visibility and voice projection (Smith and Dallman 1996). Black-throated green warblers at Calling Lake appeared to place their territory boundaries at stand edges (T. Hannah, *unpubl. data*). This may be due to a height discrepancy between adjacent stands that allows songs to be

carried further, enhances visibility, or increases thermoregulation and prey availability, as slopes do in Alaska and forest gaps do in Michigan. Previous studies (Reid and Weatherhead 1988, St.-Louis et al. 2004) have suggested territory placement may be based on landmarks such as topography or rocks as well as by neighbouring conspecifics. Whether black-throated green warblers at Calling Lake use height differences at stand edges as territory boundaries should be determined, as this may influence territory placement on the landscape beyond internal stand attributes examined in this study.

Collins (1983) investigated black-throated green warbler associations across geographically diverse habitat structures and concluded that the species does not demonstrate any consistent preference for habitat attributes, but rather exhibits plasticity depending on the vegetation type and geographic location within the range. Parrish (1995) and Whelan (2001) examined use of fine-scale foliage structure in experimental settings. They found that individual preferences for substrates depended on the habitat structure of the bird's originating location, yet they consistently foraged on the upper surfaces of leaves. Since there are regional preferences for both foliage substrates and habitat types, applying results from habitat selection studies on populations throughout the range of this species is inappropriate for formulating specific management guidelines.

3.4.2.2 Edge Avoidance

Edge avoidance was exhibited by black-throated green warblers in the forest fragments, with distances to fragment edges between 23.59-m and 31.75-m greater than distances to control site boundaries. This response could contribute to declines in abundance, through reduction of the functional area of the patch (Freemark and Collins 1992). Responses to anthropogenic edges in previous studies have been related to factors

such as prey type and availability (Jokimäki et al. 1998, Van Wilgenburg et al. 2001), vegetation structure and time of day (Mazerolle and Hobson 2003), making it difficult to determine the basis for the edge avoidance demonstrated here without direct analyses of these factors. My results suggesting edge avoidance are not consistent with conclusions from a study on other forest bird species in the region, which found no response to edges (Song 1998). In contrast, Norris et al. (2000) and Mazerolle and Hobson (2003) located individuals closer to edges than expected, citing improved foraging conditions or greater cover from predators as possible reasons. Lambert and Hannon (2000) examined ovenbird territory placement post-harvest in riparian buffer strips of varying widths, and found either no response, or edge attraction, depending on the width of the buffer strip. A review of edge effects by Harper et al. (2005) noted that the magnitude and distance of edge influence on vegetation depends on the ecotone as well as the response being measured. The avoidance distance of black-throated green warblers documented here should be evaluated in conjunction with specific vegetation components as well as detailed measurements of prey availability and predation rates. Further, an evaluation of cumulative edge effects based on proximity to multiple edges, rather than the nearest edge as measured here, may provide further insight into response to edges. Finally, I analysed edge response using individual locations within territories as a measure, rather than overall territory placement relative to edges. While this method is appropriate for gauging general behavioural response to edges by individuals, it does result in inflated sample sizes and associated issues with pseudo-replication (Hurlbert 1984). The inclusion of bird identity as a random factor in a mixed model would avoid the issue of pseudoreplication, and provide a better measure for evaluating edge avoidance.

3.4.3 Habitat Quality

No significant difference was detected in fitness between fragment and control territories, for either pairing status or reproductive success. However, the results for both pairing status and reproductive success had marginal significance levels, and low sample sizes may have reduced the power to detect biologically-relevant differences in fitness. Nonetheless, females were present and successfully breeding in the fragments, suggesting that habitat quality was sufficient to attract females, and resources existed for nesting and raising young. While the mean reproductive rank was similar between fragments and controls, the absolute number of reproductively active territories, therefore potential recruitment, was higher in controls. These results are a first step in understanding patterns of habitat quality. However, a metapopulation study examining demographics and source-sink dynamics is necessary to identify whether the fragment and control populations are self-sustaining (Opdam 1991, Hanski 1998).

A reduction in habitat quality may be compensated for by an increase in territory size to ensure an adequate supply of necessary resources, such as insect prey (Smith and Shugart 1987, Marshall and Cooper 2004) or potential nest sites (Newton 1998). However, I detected no difference in territory size between fragments and controls. This suggests that overall habitat quality did not decrease in forest fragments, and the decline is more likely a consequence of a reduction in area due to edge avoidance, coupled with narrow habitat preferences, which resulted in reduced area for territory establishment.

An unexpectedly low overlap of territory area between years was detected, with only 7.7% of occupied areas intersecting, based on delineation of territories using specified criteria of 25 locations during 3 visits each 10 days apart. This suggests low

site fidelity, which is surprising, since returning songbirds generally re-use portions of their breeding territory from previous years (Haas 1998). It is likely the habitat was not saturated, as the population is considerably reduced compared to pre-harvest abundance levels. This may lead to adjacent suitable habitat remaining unoccupied (Ward 2005), allowing a relaxation of fidelity to previous breeding sites. There is also the possibility of a change in habitat quality which was not detected in these analyses, leading to very low return rates, and thus a shift in territory placement between 2003 and 2004. Further study is required to clarify the mechanism leading to low territory overlap.

Abundance estimates from tracking surveys in controls were similar to estimates from point counts, yet in fragments, more individuals were detected from tracking surveys than point counts. Tracking most likely detected a larger proportion of non-territorial floaters in fragments. Territory delineation, based on repeated detections over a fixed time period, suggested that a greater number of territorial individuals existed in the controls than the fragments. To determine the number of floaters in the population, banding or radio-collaring of individuals and subsequent tracking is necessary. Moreover, morphological measurements could be taken with either of these techniques to assess age and body condition, as a lack of delayed plumage maturation makes it unreliable to visually distinguish second year males from older, more experienced males in the field (Rohwer and Butcher 1988). Colour-banding would ensure greater accuracy in territory delineations, and would enable assessment of site fidelity between years. However, as males consistently occupy the canopy, re-sighting rates of colour bands may be low. While constraints on battery life limit the ability of radio-collars to address issues of site fidelity, this technique may address issues relating to population

demographics. Questions could be addressed such as whether younger males are relegated to lower quality habitat, if dispersal of young is being affected by fragment isolation, and what proportion of non-territorial floaters and polygamous interactions exists in the population (Holmes et al. 1996, Zanette 2001). Target mist-netting was attempted in this study, using a decoy and conspecific playback techniques, however response was poor, with males rarely dropping to net-height from the canopy. Improved capture rates of individuals is necessary for application of these techniques.

3.4.4 Conservation and Management Implications

Long-term monitoring of a large-scale landscape experiment documented the decline in the Calling Lake black-throated green warbler population. Studies at this spatial and temporal scale are necessary to recognize patterns; however, finer-scale data on habitat use, as well as population-level surveys to determine fitness, are essential to identify causal mechanisms. My study documented fragmentation effects comprised of both area and edge effects, and thus has significant implications towards future management of the black-throated green warbler in the mixedwood boreal forest of northern Alberta. The decline in the control sites, however, suggests an even larger effect beyond the boundaries of the experiment, and requires further research regarding habitat change on the wintering-grounds and additive regional effects.

Black-throated green warblers prefer older, mixedwood forests, with components of large white spruce and large paper birch. These stands are at risk should the standard 2-pass clearcut system with a 70- year rotation, resulting in the "unmixing" of the mixedwood forests, be continued as a dominant harvesting technique (Hobson and Bayne 2000, Schneider et al. 2003). It is critical that old (~120 years) mixedwood (~12% white

spruce in the canopy) forest, containing large diameter trees (> 40-cm dbh for aspen, poplar and spruce, >20-cm dbh for birch), be maintained for black-throated green warbler population persistence on the Alberta landscape. As well, suitable forest patches should exceed 40 hectares in size, given documented area effects and edge avoidance. Only 3 patch sizes were examined here; fragments 10-ha in size were clearly insufficient for maintaining black-throated green warblers, 40-ha patches experienced steep declines, and abundance patterns over time in 100-ha patches were similar to those in controls. Patches between 40- and 100-ha should be evaluated to determine if a threshold between these sizes exists, as forest remnants may need to be closer to 100-ha in size to sustain local populations. As edge avoidance was detected, minimizing the edge to area ratio of remnant forests may aid in sustaining viable populations (Helzer and Jelinski 1999).

Most of the published literature details natural history traits from the eastern portion of the black-throated green warbler's range (ex. Collins 1983, King et al. 1997, Smith et al. 1998, Patten and Burger 1998, Whelan 2001; but see Robichaud and Villard 1999). This species demonstrates plasticity in habitat use throughout its range, yet not necessarily within a region. Due to this variation, blanket policies for conservation and management applied to a species range-wide may be inappropriate. It is imperative that population monitoring and species-specific management be focused within the region of interest.

The anthropogenic effects studied here must be framed within the context of a dynamic forested system, where matrix resistance, defined by both permeability and suitability, may decline over time (Hames et al. 2001, Schmiegelow and Mönkkönen 2002), and regenerating cutblocks may soften edges (Harper et al. 2005). It is possible

the changing matrix will allow populations to recover over time, contrary to the long-term responses observed in agricultural settings, where the matrix is permanently converted from forested habitat (Hobson et al. 2002). Nevertheless, incremental habitat loss at the landscape level may have larger impacts on local populations over time. Further monitoring of the population beyond the time frame studied here, in conjunction with both local vegetation estimates on edge contrast and cutblock regeneration, and landscape-scale measures of forest cover and habitat change, will shed light on the relative effects of local and landscape factors on the population.

3.5 Literature Cited

Alberta Environmental Protection. 1994. Alberta vegetation inventory standards manual, Version 2. Land Information Division, Resource Information Development Branch. Edmonton, AB.

Armstrong, D.P. 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. Conservation Biology 19(5): 1402-1410.

Barg, J., Jones, J., and R. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core territories. Journal of Animal Ecology 74: 139-149.

Bayne, E.M. and K.A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation on artificial nests. Conservation Biology 11(6): 1418-1429.

Bayne, E.M. and K.A. Hobson. 2001. Effects of habitat fragmentation on pairing success of ovenbirds: importance of male age and floater behavior. Auk 118(2): 380-388.

Bayne, E.M., and K.A. Hobson. 2002. Apparent survival of male ovenbirds in fragmented and forested boreal landscapes. Ecology 83 (5): 1307-1316.

Bélisle, M. and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17: 219-231.

Bender, D.J., Contreras, T.A., and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79(2): 517-533.

Beyer, H. L. 2005. Hawth's Analysis Tools for ArcGIS. [computer software]. Available at http://www.spatialecology.com/htools.

Bollinger, E.K. and P.V. Switzer. 2002. Modeling the impact of edge avoidance on avian nest densities in habitat fragments. Ecological Applications 12(6): 1567-1575.

Brigham, M. No date. Bird Sounds of Canada , Volume 3: Warblers to Sparrows. [audio CD]. In conjunction with the Canadian Museum of Nature. Mount Albert, Ontario. Holbom Dist. Co. Ltd.

Chalfoun, A.D., Thompson, F.R., and M.J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16(2): 306-318.

Chen, J., Franklin, J.F. and T.A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology 63: 219-237.

Collins, S.L. 1983. Geographic variation in habitat structure of the Black-throated Green warbler (*Dendroica virens*). Auk 100: 382-389.

Cooper, C.B. and J.R. Walters. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. Conservation Biology 16(2): 471-478.

Cotterill, S.E. and Hannon, S.J. 1999. No evidence of short-term effects of clear-cutting on artificial nest predation in boreal mixedwood forests. Canadian Journal of Forest Research 29(12): 1900-1910.

Cumming, S.G., F.K.A. Schmiegelow, and P.J. Burton. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecological Applications 10(3): 744-759.

DeLaune, M.G. 2003. Xtools ArcView Extension version 15/09/03 [computer program]. Oregon Department of Forestry, Salem, OR.

De Solla, S., Bonduriansky, R. and Brooks, R. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68: 221-234.

Desrochers, A. and S.J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11(5): 1204-1210.

Donovan, T.M., Thompson III, F.R., Faaborg, F.R. and J.R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9(6): 1380-1395.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487-515.

Flaspohler, D.J., Temple, S.A. and R.N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications 11(1): 32-46.

Freemark, K., and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pgs 443–454 *in* Ecology and Conservation of Neotropical Migrants. J. M. Hagan III and D.W. Johnston, Eds. Smithsonian Institute Press, Washington, D.C.

Freemark, K.E. and H.G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36: 115-141.

Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98(3): 447-458.

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk: 115(4): 929-936.

Hagan, J.M.III, Vander Haegen, W.M. and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188-202.

Hames, R.S., Rosenberg, K.V., Lowe, J.D. and A.A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. Journal of Applied Ecology 70: 182-190.

Hanski, I. 1998. Metapopulation dynamics. Nature 396: 41-49.

Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19(3): 768-782.

Harris, R.J. and J.M. Reed. 2001. Territorial movements of black-throated blue warblers in a landscape fragmented by forestry. Auk 118(2): 544-549.

Harris, R.J., and J.M. Reed. 2002. Behavioral barriers to non-migratory movement of birds. Annals of Zoology Fennici 39: 275-290.

Helzer, C.J. and D.E., Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications 9(4): 1448-1458.

Hemson, G., Johnson, P., South, A., Kenwards, R., Ripley, R. and Macdonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology 74: 455-463.

Hobson, K.A. and E.M. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. Condor 102(4): 759-769.

Hobson K.A., Bayne E.M., and S.L. Van Wilgenburg. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. Conservation Biology 16 (6): 1530-1541.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. Journal of Animal Ecology 65: 183-195.

Hoover, J.P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary warbler. Ecology 84(2): 416-430.

Hurblert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Ibarzabal, J., and A. Desrochers. 2001. Lack of relationship between forest edge proximity and nest predator activity in an eastern Canadian boreal forest. Canadian Journal of Forest Research 31:117-122.

Intercooled STATA for Windows, version 9.0. 2005. [computer program]. StataCorp LP, College Station, TX.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resources preference. Ecology 61(1): 65-71.

Jokimäki, J., Huhta, E., Itamies, J., and P. Rahko. 1998. Distribution of arthropods in relation to forest patch size, edge and stand characteristics. Canadian Journal of Forest Research 28: 1068-1072.

King, D.I., Griffin, C.R., and R.M. DeGraaf. 1997. Effect of clearcut borders on

distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109(2): 239-245.

Lambert, J.D. and S.J. Hannon. 2000. Short-term effects of timber harvest on abundance, territory characteristics, and pairing success of ovenbirds in riparian buffer strips. Auk 117(3):687-698.

Lampila, P., Mönkkönen, M. and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. Conservation Biology 19(5): 1537-1546.

Manly B.F.J., McDonald L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2003. Resource selection by animals - Statistical design and Analysis for field studies. Second edition. London: Kluwer academic publishers.

Marshall, M.R. and R.J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. Ecology 85(2): 432-445.

Matsuoka, S., Handel, C., Roby, D. and Thomas, D. 1997. The relative importance of nesting and foraging sites in selection of breeding territories by Townsend's warblers. Auk 114(4): 657-667.

Mazerolle, D. F., and K. A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. Auk 120(1):152-162.

McClean, S.A., Rumble, M.A., King, R.M. and W.L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62(2): 793-801.

Morse, D.H. 1967. The contexts of songs in the Black-throated green and Blackburnian warblers. Wilson Bulletin 79: 62-72.

Morse, D.H. 1970. Territorial and courtship songs of birds. Nature 226:659-661.

Morse, D. H. 2005. Black-throated Green Warbler (*Dendroica virens*). *In* The Birds of North America (A. Poole, Ed.). Cornell Laboratory of Ornithology, Ithaca, NY. [online]: http://bna.birds.cornell.edu/BNA/account/Black-throated_Green_Warbler/. (Revised August 2005).

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150: 650–661.

Nagy, L.R. and Holmes, R.T. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? Journal of Avian Biology 35: 487-491.

Neu, C.W., Byers, C.R., and J.M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541-545.

Nesby, R. 1997. Alberta vegetation inventory standards manual. Version 2.2. Alberta Environmental Protection. Edmonton, AB. 42 pp.

Newton, I. 1998. Population limitation in birds. Academic Press Ltd., London, UK.

Norris, D.R., and B.J.M. Stutchbury. 2002. Sexual differences in gap crossing ability of a forest songbird revealed through radiotracking. Auk 119: 528-532.

Norris, D.R., Stutchbury, B.J.M., and T.E. Pitcher. 2000. The spatial response of male hooded warblers to edges in isolated fragments. Condor 102(3): 595-600.

Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecology 5(2): 93-106.

Parker, T.H., Stansberry, B.M., Becker, C.D. and P.S. Gipson. 2005. Edge and area effects on the occurrence of migrant forest songbirds. Conservation Biology 19(4): 1157-1167.

Parrish, J.D. 1995. Experimental evidence for intrinsic microhabitat preferences in the black-throated green warbler. Condor 97: 935-943.

Patten, M.A. and J.C. Burger. 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. Canadian Journal of Zoology 76: 433-439.

Reid, M.L. and P.J. Weatherhead. 1988. Topographical constraints on competition for territories. Oikos 51: 115-117.

Robichaud, I.R. and M.-A. Villard. 1999. Do black-throated green warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101: 262-271.

Rodgers, A.R. and A.P. Carr. 1998. HRE: The Home Range Extension for ArcView (Beta test version July 1998). User's Manual. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, ON.

Rohwer, S. and G.S. Butcher. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. American Naturalist 131(4): 556-572.

Schmiegelow, F.K.A., Machtans, C.S. and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78(6): 1914-1932.

Schmiegelow, F.K.A. and S.J. Hannon. 1999. Forest-level effects of management on boreal songbirds: the Calling Lake fragmentation studies. *In* Forest fragmentation: wildlife and management implications, pp 201-220. Edited by J.A. Rochelle, L.A. Lehmann and J. Wisniewski. Brill, Boston, MA.

Schmiegelow, F.K.A. and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12(2): 375-389.

Schneider, R.R., Stelfox, J.B., Boutin, S., and S. Wasel. 2003. Managing the cumulative impacts of land uses in the western Canadian sedimentary basin: a modeling approach. Conservation Ecology 7(1): 8.

Sillett, T. S., Rodenhouse, N., and Holmes, R. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecology 85(9): 2467-2477.

Smith, R. and M. Dallman. 1996. Forest gap use by breeding Black-throated Green warblers. Wilson Bulletin 108(3): 588-591.

Smith, R., Hamas, M. and M. Dallman. 1998. Spatial variation in foraging of the Black-throated green warbler along the shoreline of northern Lake Huron. Condor 100: 474-484.

Smith. S.M. 1995. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? Ecology 76(6): 1997-1998.

Smith, T.M., and H.H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68(3):695-704.

Song, S.J. 1998. Effect of natural and anthropogenic edge on songbirds breeding in the boreal mixed-wood forest of Northern Alberta. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Song, S.J. and S.J. Hannon. 1999. Predation in heterogeneous forests: A comparison at natural and anthropogenic edges. Ecoscience 6(4):521-530.

SPSS for Windows version 13.0. 2004. [computer program]. SPSS Inc., Chicago, IL.

St.-Clair, C.C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. Conservation Biology 17(4): 1151-1160.

St-Louis, V., Fortin, M.-J., and Desrochers, A. 2004. Spatial association between forest heterogeneity and breeding territory boundaries of two forest songbirds. Landscape Ecology 19: 591-601.

Swihart, R.K., and N.A. Slade. 1985. Influence of sampling interval on estimates of home range size. Journal of Wildlife Management 49:1019-1025

Thomas, D.L. and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54: 322-330.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Van Wilgenburg, S. L., Mazerolle, D.F., and K.A. Hobson. 2001. Arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: Implications for forest birds. Ecoscience 8: 462-470.

Vickery, P.D., M.L. Hunter, Jr. and J.V. Wells. 1992. Use of a new reproductive index to evaluate the relationship between habitat quality and breeding success. Auk 109(4): 697-705

Villard, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk 115(3): 801-805.

Ward, M.P. 2005. The role of immigration in the decline of an isolated migratory bird population. Conservation Biology 19(5): 1528-1536.

Whelan, C.J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82(1): 219-231.

Willson, M.F. 2004. Loss of habitat connectivity hinders pair formation and juvenile dispersal of Chucao Tapaculos in Chilean rainforest. Condor 106(1): 166-171.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Young, L., Betts, M.G., and A.W. Diamond. 2005. Do Blackburnian warblers select mixed forest? The importance of spatial resolution in defining habitat. Forest Ecology and Management 214: 358:372.

Zanette, L. 2000. Fragment size and the demography of an area-sensitive songbird. Journal of Animal Ecology 69: 458-470.

Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. Journal of Avian Biology 32(1): 38-46.

Zanette, L., Doyle, P., and S.M. Tremont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81(6): 1654-1666.

Zar, J.H. 1999. Biostatistical Analysis. Prentice-Hall, Inc. Upper Saddle River, NJ.

Chapter 4

DECLINES IN THE BLACK-THROATED GREEN WARBLER: CONCLUSION

4.1 THESIS SUMMARY

Black-throated green warblers have been identified as a species of concern in Alberta due to sensitivity to projected habitat loss and fragmentation. This study documented the pattern, and explored the process underlying the decline of the black-throated green warbler population at Calling Lake, Alberta, in response to experimental forest harvesting. Long-term surveys, and intensive short-term population monitoring, enabled an assessment of area and edge effects, habitat associations and measures of habitat quality.

Eleven years post-harvest, relative abundance levels of black-throated green warblers at Calling Lake, as sampled by point count surveys, were 70% below pre-harvest levels, with both isolated fragments and continuous controls experiencing significant declines. Coarse-scale determinants of local patch occupancy included pre-harvest abundance and measures of forest structure; spatial habitat structure (e.g. patch size and treatment) did not contribute significantly to the explained variation. Higher occupancy occurred in older stands (>100 years) containing white spruce in the overstory (>5% canopy composition), and occurred at sites with higher pre-harvest abundance. Coarse-scale models were effective in identifying local, high-quality sites, as measured by frequency of occupancy, but more detailed population and habitat measures were required to explain local declines, and predict the consequences of regional habitat change.

I documented an area effect at Calling Lake, whereby abundances in10-ha fragments collapsed within 3 years of harvest, and steep declines in black-throated green warbler abundance occurred in 40-ha fragments, compared with the larger fragments (100-ha) and all controls sizes. Mean distance of territories to site edge was ~27-m greater in the fragments relative to control sites, also suggesting edge avoidance. No significant difference was observed in mean territory size, pairing status, or reproductive success between fragments and controls, although small sample sizes resulted in low power to detect effects, and significance levels were marginal. Abundance estimates suggest control sites supported a greater number of territorial birds, and therefore had greater net productivity.

Habitat selection was measured at two spatial scales to identify selected attributes within black-throated green warbler territories, and evaluate whether these attributes had experienced differential change between fragments and controls. Black-throated green warblers used white spruce more than expected for foraging and singing, consistent with previous research in Alberta (Robichaud and Villard 1999). However, I also identified a preference for nesting in paper birch, which contributes new information on the breeding ecology of this species. All trees used by black-throated green warblers had larger diameters than available trees, supporting previously documented associations with older forests (Robichaud and Villard 1999, Vernier et al. 2002). As tree age, height, and dbh are correlated, a selection for one attribute may indicate a selection for another attribute. Territories were established in older stands (averaging 120 years) with greater amounts of white spruce (averaging 12%) than random, consistent with results from my coarse-scale occupancy model. Differential change between fragments and controls in vegetation

attributes selected by black-throated green warblers occurred for white spruce 23.1-38.0 cm dbh (increased in fragments, with no change in controls), and >38.0 cm dbh trembling aspen (no change in controls, but decreased in fragments). However, as these particular tree species and size classes were not selected for specific behaviours, it is unclear whether these changes contributed to the observed decline in fragments relative to controls.

I suggest the midterm (5-years post-harvest) decline observed in the isolated forest fragments was due primarily to a combination of area and edge effects. Smaller isolated patches exhibited the greatest rate of decline, and edge avoidance in fragments reduced the functional area of these patches. However, the longer term decline in the controls indicates a possible regional effect external to the fragmentation experiment. Factors such as weather effects, regional habitat loss, and habitat alteration on wintering grounds may be responsible for overall population declines, and should be further explored.

4.2 Management Recommendations

Within a territory, black-throated green warblers selected large diameter white spruce (~47.8 cm) within deciduous-dominated stands. Emergent white spruce in "pure" deciduous stands may be underestimated in forest inventories, and overlooked by forest planners (Cumming et al. *unpubl. manuscript*), which may have consequences when identifying priority areas for conservation of this species. Large diameter paper birch (~21.4 cm dbh) were also identified as important for the nesting requirements of the black-throated green warbler, yet no specific management guidelines exist for this tree species. In fact, paper birch has been identified as a species lacking provisions for

maintenance in post-harvest stands in Alberta (Alberta Reforestation Standards Science Panel 2001). Given the significance of large paper birch and large white spruce to black-throated green warblers, efforts should be made to ensure both are accurately accounted for in forest planning in order to effectively manage black-throated green warbler populations.

At the stand-level, black-throated green warblers occupy older (~100-130 years), mixedwood (~5-20% white spruce) stands in the western boreal forest. This is a vulnerable habitat type given conventional forest management strategies. Short harvest rotations are reducing the amount of older forests on the landscape, as stands are harvested before they exhibit old-growth characteristics (Stelfox 1995). Current silvicultural prescriptions create even-aged, single-species stands (Hobson and Bayne 2000), as these stands have a greater economic potential than mixedwood stands (Grover and Greenway 1999). Innovative forest management strategies involving mixedwood management, which maintains both deciduous and conifer components in regenerating stands, and integrated landscape management, which minimizes edge creation by reducing the industrial footprint on the landscape, could contribute significantly to maintaining suitable habitat for this species.

Harvest planning should ensure patches of suitable habitat >40-ha are maintained, as habitat fragments 40-ha and less in size exhibited steep declines in abundance of black-throated green warblers. However, all else remaining equal, a corollary of leaving larger remnants may be the presence of larger cutblocks, which may impede dispersal, affecting the colonization and recruitment of remaining intact areas (Lichstein et al. 2002). Forest harvest planning should endeavour to leave larger areas of undisturbed

forest, and minimize both the isolation of the remnant patches as well as their edge-to-area ratio (Saunders et al. 1991). This may involve aggregating harvest blocks, as well as reducing the overall amount of harvest at the landscape level. Corridors may potentially mitigate the effects of fragmentation, especially for species that are gap-sensitive, however their efficacy in this system is uncertain (Hannon and Schmiegelow 2002). The amount and configuration of habitat at the landscape-level necessary for black-throated green warbler population persistence is unknown, and should be further evaluated to ensure appropriate spatial harvest planning.

4.3 FUTURE RESEARCH

4.3.1 Calling Lake Black-throated Green Warbler Research

Study-wide surveys should be continued in order to document the population trend as it responds to matrix regeneration, forest succession, and further regional habitat loss resulting from ongoing forest harvest in the surrounding landscape. The increasing presence of linear features associated with energy sector activities within the study area may influence bird behaviour, as songbirds may adjust territory boundaries in relation to linear features (Bayne et al. 2005) or may avoid crossing gaps (Bélisle and Desrochers 2002). Ensuring the controls remain undisturbed allows the reference sites to remain true experimental controls, and enhances their value as long-term benchmarks.

Further population-level research at Calling Lake should include intensive nest-monitoring to determine if productivity (numbers of successfully fledged young) is consistent across all sites. Colour-banding would be useful to identify individuals, thereby increasing the accuracy of territory delineations. This would also allow an assessment of site fidelity between years, which may be very low, given the low

incidence of territory overlap between 2003 and 2004. Such information would contribute to exploration of potential regional source/sink dynamics. Colour-banding would also reveal the number of non-territorial floaters, whose presence was suggested by contrasting abundance estimates determined through two different survey techniques, tracking and point counts, with elevated numbers of floaters recorded in fragments. Radio-telemetry would provide additional opportunities to document extra-territorial movements (e.g. Norris and Stutchbury 2001), and female dispersal to isolated fragments, which may be affected by patch isolation (Cooper and Walters 2002). As well, patch isolation could influence natal dispersal (Svein 2001), which could affect future recruitment and patch productivity, and requires radio-telemetry for effective evaluation. Examining movement between isolated and continuous forest patches could reveal additional negative impacts of forest fragmentation beyond area and edge effects, and increase the knowledge base for this species, which is limited in many areas (Morse 2005).

4.3.2 Additional Black-throated Green Warbler Research

Patches of habitat over a broader range of size classes, particularly between 40-ha and 100-ha, should be evaluated to determine if a size threshold for ameliorating area effects exists. As this may be logistically difficult to execute in a landscape experiment, response of songbirds to natural isolates may be used as surrogates for a manipulated design. Schmiegelow (1997) used this approach, examining songbird abundance in deciduous-dominated patches naturally isolated from similar habitat by black spruce stands. She found that black-throated green warblers were absent from small isolates ($\bar{x}$ = 2.9-ha), and were present in only the 2 largest isolates ($\bar{x}$ = 38.1-ha), consistent with my

findings. However the isolates supporting black-throated green warblers were relatively near (40-90-m) additional patches of deciduous-dominated patches, thus the effects of isolation could not be evaluated for this species. Research incorporating natural isolates should attempt to vary both patch size and isolation distance to partition the influence of these factors.

Both the amount and configuration of habitat on the landscape have proven to be significant determinants of local abundance for many songbirds (e.g., Andrén 1994, Villard et al. 1999). Schmiegelow and Cumming (2004) report that the local abundance of black-throated green warblers was negatively affected by increased density of linear features, such as roads and pipelines, at a landscape-level (100 km^2). Vernier et al. (2002) found black-throated green warbler abundance at Calling Lake to be associated with only 1 local (100-m radius circular buffer) variable, yet 5 neighbourhood (400-m wide donut around the local buffer) variables, demonstrating the importance of multi-scale analyses to identify all potential influences. Attempts should be made to ascertain whether the decline in the control sites can be attributed to factors external to the Calling Lake Fragmentation Experiment, such as regional loss of mixedwood habitat or wintering-ground habitat change.

Point count surveys identified patterns of occupancy related to stand age and composition, which were also evident from finer-scaled territory mapping. However edge avoidance and the importance of paper birch for this species, both of which have important implications for forest management, were only detected through population-level research. Ideally, research should be long-term, and conducted at multiple scales, in order to understand variation in responses of forest songbirds to local and landscape

patterns (McGarigal and Cushman 2002). Population monitoring should occur regionally, as range-wide variation in habitat selection exists (Morse 2005), and should not be limited to roadside surveys, as these may not effectively survey forest interior songbirds (Schmiegelow and Mönkkönen 2002). The ~70% decline of the black-throated green warbler population at Calling Lake is dramatic, and if representative of regional responses to forest harvesting, raises serious concerns about the long-term persistence of this species in this system. While this species has been listed in Alberta as a species of concern (Norton 1999), measures have yet to be implemented to mitigate further declines. Documenting this pattern and elucidating the underlying mechanisms can inform the development and implementation of management strategies to maintain habitat for this species in the western boreal forest.

4.4 Literature Cited

Alberta Reforestation Standards Science Panel. 2001. Linking regeneration standards to growth and yield and forest management objectives. Report submitted to Alberta's Minister of Sustainable Resource Development. August 29, 2001.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71(3): 355-366.

Bayne, E.M., Van Wilgenburg, S.L., Boutin, S. and K.A. Hobson. 2005. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape ecology 20(2): 203-216.

Bélisle, M. and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17: 219-231.

Cooper, C.B. and J.R. Walters. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. Conservation Biology 16(2): 471-478.

Cumming, S.G., Trindade, M., Greene, D., and E. MacDonald. 2004. Canopy and emergent white spruce in "pure" deciduous stands: frequency, causes, and ecological importance. *Unpublished manuscript.*

Grover, B.E. and K.J. Greenway. 1999. The ecological and economic basis for mixedwood management, pp. 419-428 i*n* T.S. Veeman, D.W. Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin (Eds.). Proceedings of the 1999 Sustainable Forest Management Network Conference, Sustainable Forest Management Network, Edmonton, Alberta, Canada

Hannon, S.J. and F.K.A. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. Ecological Applications 12(5): 1457-1468.

Hobson, K.A. and E.M. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. Condor 102(4): 759-769.

Lichstein, J.W., Simons, T.R., and K.E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications 12(3): 836-857.

McGarigal, K. and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12(2): 335-345.

Morse, D. H. 2005. Black-throated Green Warbler (*Dendroica virens*). *In* The Birds of North America (A. Poole, Ed.). Cornell Laboratory of Ornithology, Ithaca, NY. [online]: http://bna.birds.cornell.edu/BNA/account/Black-throated_Green_Warbler/. (Revised August 2005).

Norris, D.R. and B.J.M. Stutchbury. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. Conservation Biology 15(3): 729-736.

Norton, M.R. 1999. Status of the black-throated green warbler (*Dendroica virens*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 23, Edmonton, AB. 24 pp.

Robichaud, I.R. and M.-A. Villard. 1999. Do black-throated green warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. The Condor 101: 262-271.

Saunders, D.A., Hobbs, R.J. and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1): 18-32.

Schmiegelow, F.K.A. 1997. The effect of experimental fragmentation on bird community dynamics in the boreal mixedwood forest. PhD. Dissertation. University of British Columbia, B.C.

Schmiegelow, F.K.A. and S.G. Cumming. 2004. The Remote Areas Project: a retrospective study of avian indicators of forest change. Sustainable Forest Management Network Project Report 2003/04.

Schmiegelow, F.K.A. and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12(2): 375-389.

Stelfox, J.B. 1995. Introduction *in* Stelfox, J.B. (Ed.), Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environment Centre, Vegreville, AB. AECV95-R1 pp.1-12.

Svein, D. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92(2): 344-356.

Vernier, P.R., Schmiegelow, F.K.A. and S.G. Cumming. 2002. Modeling bird abundance from forest inventory data in the boreal mixed-wood forests of Canada. Pp. 559-571 *in* Scott, J.M., Heglund, P.J., Morrison, M., Raphael, M., Haufler, J., and B. Wall (Eds.). Predicting species occurrences: issues of scale and accuracy. Island Press, Covello, CA.

Villard, M.-A., Trzcinski, M.K. and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13(4): 774-783.